

THE ECOLOGY OF A RELIC HYBRID OAK
IN THE GREAT BASIN AREA OF UTAH

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THE ECOLOGY OF A RELIC HYBRID OAK
IN THE GREAT BASIN AREA OF UTAH

by

Rudy Drobnick

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INTRODUCTION

On May 23, 1954, the writer observed on a south-facing slope in Harker's Canyon situated in the Oquirrh Mountains, about 12 miles west of Salt Lake City, a large clone* of oak strikingly different from the colonies of Gambel oak surrounding it. The feature that led to this discovery was a great accumulation of unusually small, dry and hard leaves that had apparently fallen from the oak stems since the melting of winter snows. Such a feature contrasts sharply with the shedding habit of Gambel oak which is deciduous in late fall. Other clones both higher and lower in elevation than the first, were discovered in Harker's Canyon and elsewhere. At a distance these could be distinguished from Gambel oak by their erect, intensely dense branches and the noticeably bluish-green cast of their foliage in summer. Closer examination of these clones revealed rigid branches and small holly-like leaves, elliptical, spinulose-dentate with 3-6 large teeth to a side. The retention of colored and dried leaves in fall and winter furnished a particularly striking feature which made it possible to distinguish readily, these and other clones from the early deciduous Gambel oak. A brief report of this oak was made

*The term "clone" as used in this paper designates an aggregate of aerial shoots connected by underground stems or rhizomes, all having arisen through vegetative proliferation from a single parent plant of acorn origin. Two or more clones form a "colony", and if united into a common thicket, a "clump".

by Dr. Walter P. Cottam and the author in the Utah Academy of Sciences Proceedings in 1955. The subsequent determination of this oak as a hybrid, Quercus gambelii Nutt. x Quercus turbinella Greene., was made originally by Dr. C. H. Muller, University of California at Santa Barbara, and later confirmed by Dr. John M. Tucker, University of California at Davis.

Dr. Cottam and Dr. Tucker, in the authors absence, made joint explorations in various areas of southern Utah and northern Arizona to study the affinities of this hybrid oak. Publications of their data pertinent to this study, concerning the Paleoclimatic Ecology and the Taxonomy respectively, will be available in 1958.

Explorations by the author in fall, winter and spring of 1954-55, summer and fall of 1957 and spring of 1958 revealed many similar clones on mountain ranges bordering the eastern limits of prehistoric Lake Bonneville. This area coincides with the western continuous limits of Gambel oak in the northern, central and southwestern part of Utah. Specific areas which have been explored include: the lower west face of the Wasatch Mountains from Brigham City to Nephi; the north and south drainages of the Traverse Mountains; nearly all lower drainages of the Oquirrh and Sheeprock Mountains; the majority of the lower west and southeast drainages of the Canyon Mountains; the lower west drainage of the Pahvant Mountains from Scipio to Fillmore, and Kanosh to Cove Fort, and the

southeast and lower west drainage of the Mineral Mountains northeast of Milford. These ranges support Gambel oak and scattered hybrid clones. Other ranges which apparently do not support oak of any kind were also explored. They include: nearly all lower drainages of the Stansbury Mountains; the lower north, west and south drainages of the Onaqui Mountains; the Cedar Mountains; the lower east and northwest drainages of the Simpson Mountains; the North, East and West Tintic Mountains; the Gilson Mountains; the south drainage of the San Francisco Mountains; and a portion of the lower east and southwest drainages of the Wah Wah Mountains. A survey was made on the Black Mountains southwest of Beaver, which support some Gambel oak; the Needle Mountains west of Milford where only a few isolated colonies of Gambel oak exist immediately south of Indian Peak; and the lower east and southeast drainages of the Pine Valley Mountains, which support an abundance of both parents, Q. gambelii and Q. turbinella, and many hybrids. The northern limit of live oak, Q. turbinella, is found on the Pine Valley Mountains west of Kanarraville, where relatively few colonies remain within the Great Basin drainage.

The existence of these hybrid clones in the Great Basin beyond the present limits of Q. turbinella raises problems of origin highly perplexing to the student of plant geography. When and where did these hybrid clones originate and under what climatic conditions? If they represent products of hybridization between Q. gambelii x Q. turbinella, how did they

become established? What can account for the absence of the obviously necessary live oak parent? These problems have been under investigation since 1954 and available evidence now indicates that these hybrid clones in the Great Basin are relics of an ancient, once continuous oak flora that existed in this area when the climate was warmer than at present. This study will be concerned mainly with the location, description and ecological aspects of these relic hybrid clones within the Great Basin of Utah.

REVIEW OF LITERATURE

Numerous chromosome counts have been made in the genus Quercus and all known species of Quercus are now reported to have 24 chromosomes which vary only slightly in size and morphology.^{14, 23} These cytological facts help to explain why interspecific crosses occur so readily in so many species of oak. Generally, hybrids from various species of oak are fertile and give rise to moderately vigorous F_2 individuals, the acorns of which are usually infertile.²⁴ According to Stebbins,²⁴ hybrid swarms are common in this genus. Evolution²⁶ has proceeded in this group from the Cretaceous period until the present mainly by hybridization and to a lesser extent by mutation.

Many hybrid oaks are produced under natural conditions.¹⁹ Stebbins¹⁴ states that in California, hybridization occurs in the range of overlap between Q. garryana Hook. and Q. douglasii, H. & A. At the southern end of the range of Q. douglasii, hybridization also occurs with Q. dumosa Nutt. and the closely related Q. turbinella Greene.

Another more striking example of hybridization, between morphologically dissimilar oak species are the hybrids between the evergreen, narrow-leaved and small fruited Q. virginiana Mill. and the deciduous, broad-leaved and large fruited Q. lyrata Walt. Palmer¹⁴ states that this hybrid occurs frequently in nature. Trelease²⁶ reported a total of 51 hybrids

in the United States, usually with characters intermediate between their assumed parents.

Artificially produced hybrids between Q. lyrata and Q. virginiana, Sub-Genus Lepidobalanus, White Oaks, were produced in 1909. Ness¹⁴ pollinated Q. lyrata with pollen from Q. virginiana and obtained three hybrid plants resembling Q. virginiana. In 1910 the cross was repeated and he obtained five hybrid plants. The hybrids were semi-evergreen and grew rapidly. In 1919 they produced acorns after open pollination, and twenty-three F₂ plants were obtained. Yarnell¹⁴ studied the F₂ generation and found that the plants formed two distinct groups, one similar to the virginiana parent, the other with leaves somewhat smaller, but similar to the lyrata parent. Similar characters may be observed in descriptions of various relic hybrid clones of this study, to be discussed below.

Artificial hybridization between oak species of different sub-genera yielded more striking results. Irgens-Moller¹⁴ reports that S.S. Pjatnitskii claims to have obtained under controlled conditions hybrids between the two sub-genera, Lepidobalanus (White Oaks) and Erythrobalanus (Red Oaks), by pollinating Q. robur Linn. and Q. macranthera Fisch. & Mey. with pollen of Q. borealis maxima Ashe. The F₁'s were reported to exhibit vigorous growth the first year. Among other combinations he made, hybrids of Q. macranthera x Q. robur and Q. macranthera x Q. alba Linn. yielded the highest number of acorns. It is evident that oaks within the Sub-Genus Lepidobalanus

are more likely to hybridize, since only one year is required for pollination and fruit maturation. In Erythrobalanus, two years are required for the pollination and fruit maturation process.

The genetic makeup controls most morphological differences in oaks, but variation may exist between leaves on the same plant. Abnormal leaves are often found on sterile branches, young stems, and adventitious shoots. Variation in response to environmental factors often causes growth of dissimilar leaves.²⁴ An example of leaf variations is exhibited by dimorphic foliage on various relic hybrid clones, described later in detail.

ANALYSIS OF HYBRIDIZATION
BETWEEN QUERCUS GAMBELII AND QUERCUS TURBINELLA

Detailed analyses of hybridization¹ under natural conditions have shown that one of its most common results is repeated backcrossing of hybrids to one or both parents. The characters of F₁ hybrids are similar and usually intermediate between those of the parents. With each successive backcross, the hybrid nature of the resulting offspring becomes less apparent. This process was discussed by Anderson and Hubricht¹ in 1938 and named "introgressive hybridization." Its results were described as the "introgression" of one species into another. Introgression has since been investigated in various genera of the higher plants.

Introgressive hybridization is well illustrated by the relic hybrids Quercus gambelii x Quercus turbinella, and repeated backcrosses. Observation of these relic hybrid oaks frequently reveals colonies, made up of several different plants or clones, which are probably products of F₁ hybrids or later generations backcrossing to Gambel oak, because many plants retained only a few hybrid characteristics. The remaining characteristics of these backcrosses were similar to those of Gambel oak.

The offspring of F₁ hybrids or later generations backcrossed to both parents, observed on the Pine Valley Mountains west of New Harmony, illustrate similar introgression and also

various habitat requirements of these species, hybrids and backcrosses. Live oak, Q. turbinella is the predominate species on the warm dry south exposure of an east-west directional ridge at 5500 to 6000 feet elevation. Gambel oak, Q. gambelii thrives in a cooler habitat on the north exposure. Within a very narrow strip along the ridge where both types are equally abundant and nearly meet, the conditions and location permit the formation and growth of many hybrids. Clones with foliage characters intermediate between F₁ hybrids and Q. turbinella exist on the south exposure near the ridge apex. Here they receive sunshine nearly all day similar to the requirements of Q. turbinella. Higher, at 6500 feet where the ridge joins a high southwest axis of the Pine Valley Mountains to the south, there is a swarm of hybrid derivatives consisting apparently of F₁ hybrids backcrossed to Q. gambelii. At this location they receive sun in the morning and shade in the afternoon, intermediate, but approaching more nearly the optimal conditions for Q. gambelii. This distribution pattern indicates that habitat requirements of these hybrids and various backcrosses are intermediate between those of their parents.

A heterogeneous flora of both parents, F₁ hybrids and backcrosses exists on a south exposure of the Pine Valley Mountains near Oak Grove at elevations of 6000 to 8000 feet. The optimum elevation for Q. turbinella is usually below 6000 feet, but in this area of protected warmth, the

requirements of both parents, hybrids and backcrosses exist and permit a mixed oak flora, which is less common at lower elevations of more open topography.

DESCRIPTION OF PARENTS AND HYBRIDS

Both parents belong to the Sub-Genus Lepidobalanus, White Oaks, based upon the following characters. Shell of the fruit not tomentose within; abortive ovules basal; cup scales much thickened basally, narrow at apex; stigmas short and broad; leaves if toothed not aristate; bark commonly gray and scaly or flaking.¹⁵ Pollination and fruit maturation require only one year.²⁶

Quercus gambelii Nutt.²² is usually a shrub from four to twenty feet in height forming thickets by vigorous rhizomes. Bark is from one-half to three-fourths of an inch in thickness, deeply divided into broad irregular often connected flat ridges, separating on the surface into thin dark gray scales frequently tinged with red or light brown. The wood contains conspicuous medullary rays. The buds are ovate, acute or obtuse about one-eighth of an inch in length, covered with light chestnut brown pubescent scales. Mature leaves are thick and firm, glabrous or rarely stellate pubescent, lustrous and dark or yellow-green, or dull green above, and paler, often yellowish and soft pubescent beneath. Leaves are variable, usually deeply lobed, three to five inches long and one to five inches wide, with prominent pale midribs, hairy on the underside and occasionally on the upper surface. The leaves are attached on stout petioles flattened above, and turn scarlet or orange color (copper-brown) before falling in autumn. The stipules are linear, thin and dry, dark brown

with long pale hairs, and fall early. The flowers appear in April with unfolding of new leaves or in May and June when the leaves are nearly half grown. The male flowers are borne in slender hairy aments (catkins) in the axils of ovate acute bracts about twice as long as the hairy yellow calyx, which is divided into five or six acute lobes, shorter than the stamens. Anthers are emarginate (grooved), yellow and glabrous. The bright red pistillate flowers are sessile or short stalked, and solitary or in elongated few-flowered spikes, with ovate rounded involucreal scales coated with soft pale tomentum, and acute calyx lobes. The acorns are sessile or pedunculate (stalked) and ripen in August and September. The nut is usually oval, broad at the base, obtuse and rounded or sometimes narrowed and acute at the apex, which is covered with a rusty pubescence, and usually about three-fourths of an inch long and five-eighths of an inch broad. Occasionally the acorns are more than one inch long. When ripe the acorns are dark brown and later turn light chestnut color. The cups are saucer shaped; cup shaped or rarely turbinate, enclosing one third of the nut. They are light brown and pubescent on the inner surface, coated on the outside with pale gray tomentum. The ovate scales are thickened at the base.

Quercus turbinella Greene. is an intricately branched rigid shrub, with stout stems covered by pale gray bark, usually from six to eight feet in height, often forming dense thickets. Winter buds are oval, generally acute, from

one-sixteenth to one-eighth of an inch long and covered by thin pale red scales with soft spreading and marginal hairs.²²

Mature leaves are stiff and leathery, dull bluish-green, persistent, small 3.0 x 1.5 cm., elliptical oblong, with rounded base, frequently repandly dentate with spinescent teeth. Stellate pubescence, present on both surfaces of the leaves, is more dense beneath. The leaves are attached by stout petioles rarely more than one-eighth of an inch in length.²⁶ Stipules are linear obovate or lanceolate, thin and dry, light brown, coated with pale hairs, and fall early. The flowers are produced in early spring with unfolding of new leaves. Staminate flowers are borne in pubescent aments and the pistillate flowers are sessile or pedunculate. The calyx of the staminate flower consists of four to eight ovate-lanceolate hairy sepals shorter than the stamens. The stamens are composed of slender filaments and glabrous yellow anthers. The involucral scales and the calyx of the pistillate flower are covered with pale tomentum and the stigmas are red. The acorns are usually solitary, and are sessile or short pedunculate. The nut is oval, broad at the base, usually 2.5 x 1.0 cm. (infrequently one and one-half inches in length). The cup enclosing one third of the nut, is turbinate or cup shaped, light brown and pubescent within, covered by ovate pointed scales much thickened basally and coated with pale or rufous (reddish-brown) tomentum.²²

The description of Quercus hybrid (Q. gambelii Nutt. x Q. turbinella Greene) also includes backcrosses, Q. hybrid x Q. gambelii Nutt., repeated backcrosses, and possibly F₂ individuals, Q. hybrid x Q. hybrid. Except for intermediate variable forms, colors, and persistence of leaves; the presence of stellate pubescence on young branches and leaves; the rigid, stiff branches with strong wood; and the size and shape of acorns; the remaining descriptive characters for bark, buds, (catkins, male and female flowers)* and fruit are not readily distinguishable from those of Q. gambelii Nutt.

New leaves and flowers appear at generally the same time as Gambel oak. Leafing of Q. gambelii under similar environmental conditions is variable, showing genetic differences. Therefore, hybrids also would be expected to differ. Flowering occurred on hybrid clone #24 (68) May 1, 1955, while leaves and flowers of clone #1 (2) did not appear until three weeks later. On clone #24, drooping branches less than six inches from the ground flushed leaves and flowers 7 to 10 days earlier than vertical branches, probably the result of increased temperature due to solar reradiation. Although temperatures influence the time of leafing at different elevations, differences in time of leafing among clones in similar habitats result from the individual genetic makeup of each clone.

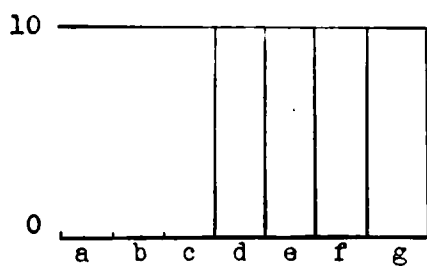
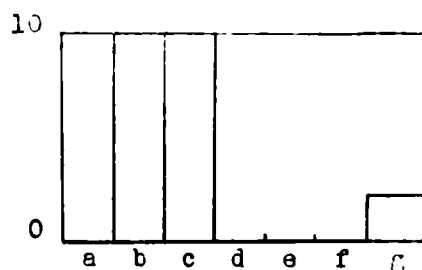
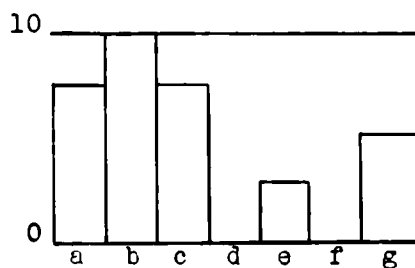
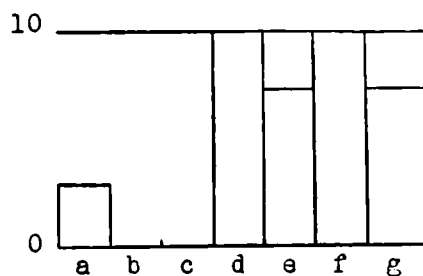
A typical example of various leaf characters is shown graphically on plate 1. Arbitrary values from zero to ten units

*Based on the inflorescence of clones #23 and #24 only.

were assigned obvious characters to illustrate a comparison of the parents, a F₁ hybrid and a backcross to Gambel oak. Only with complete collections of all relic hybrid clones in spring, summer and autumn could the total degree of parental resemblance be determined.

Morphological foliage characters such as leaf shape, texture, color and duration of persistence, which are most easily recognizable in the field, and relative abundance and structure of microscopic stellate (star-shaped) pubescence on leaves, are characters which will be used to categorize "individual" clones within colonies. It seems apparent that numerous microscopic stellate hairs with usually eight or more (16) filaments radiating outward in a flattened plane parallel to the leaf surface, in addition to the relatively small stiff, spinescent-toothed bluish-green leaves and gray bark, will ultimately separate Q. turbinella Greene; that large deeply lobed leaves of weaker texture usually shiny chlorophyll green on the surface with pubescence mostly two and four-rayed, radiating out and up at an angle from the leaf surface will ultimately separate Q. gambelii Nutt.; and intermediate leathery, green or bluish-green, shiny or dull, toothed or lobed, leaves with stellate hairs one through sixteen rayed, radiating out flat or up at an angle, with leaves persistent and retaining color until at least 7 November, are characters that will ultimately separate the various hybrids and backcross generations

from the parents. Even for a trained taxonomist, identification of these species, F_1 hybrids and backcross generations may be a hazardous venture.

Q. gambelii Mutt.Q. turbinella Greene.Clone #1(2) F₁ hybrid, Q. gambelii x Q. turbinella.Clone #1(1) Backcross, F₁ hybrid x Q. gambelii

a = leaf persistence	c = spinulose-toothed	f = shiny
b = bluish-green	d = green	g = size
	e = lobed	

Graphic illustration of some evident leaf characters in the parents, an F₁ hybrid and a backcross.

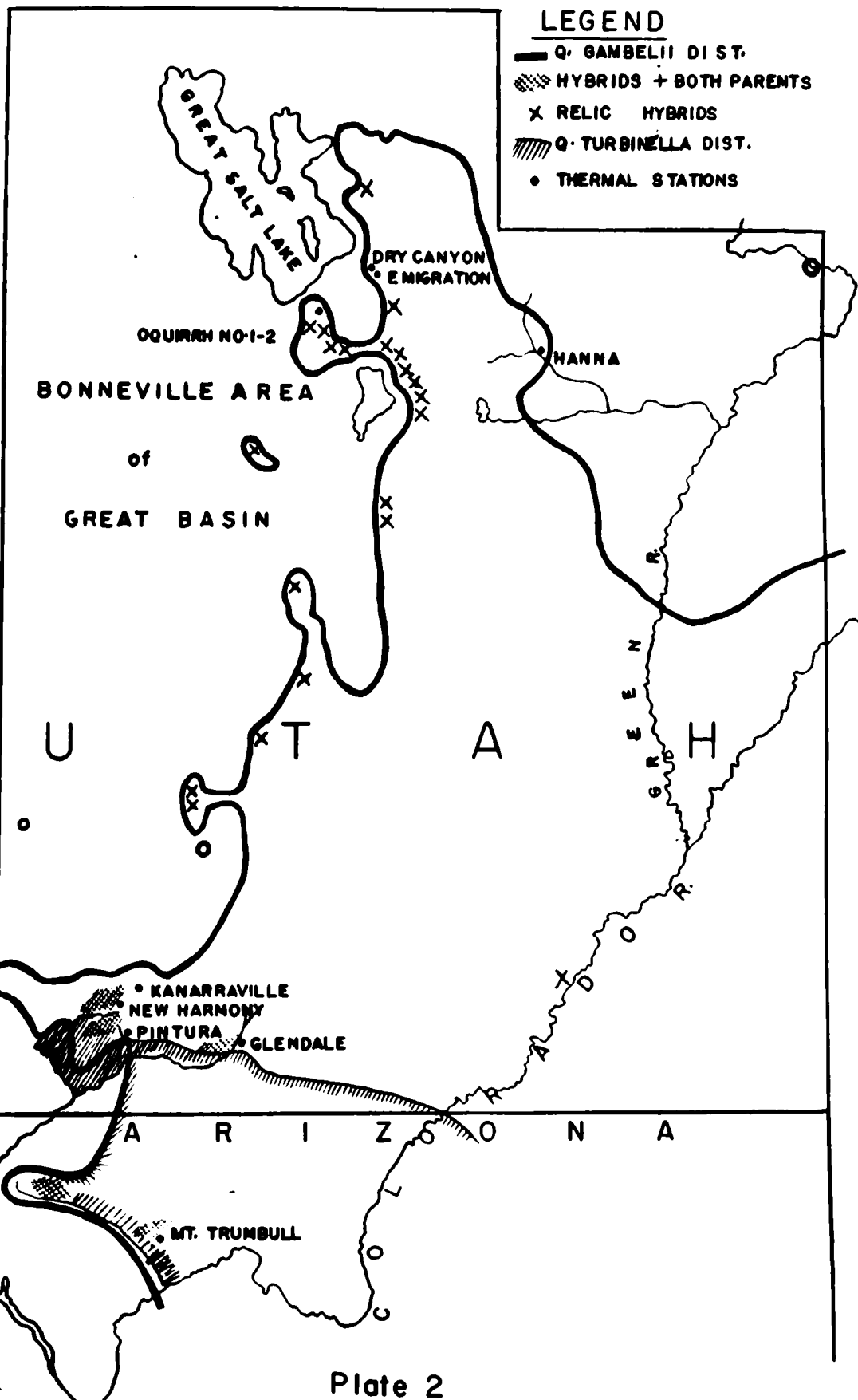




Fig. 1. The northern most clone #33, southeast of Ogden between Beus and Birch Creek Canyon in the Wasatch Mountains.



Fig. 2. Clone #23 near the mouth of Dry Creek Canyon northeast of the University of Utah.



Fig. 3. Colony #21 in George's Hollow east of the University of Utah.



Fig. 4. Colonies #11 and #11A near Big Hollow northeast of Alpine.



Fig. 5. Colony #13 at the base of Mahogany Mountain east of Lindon.



Fig. 6. Colony #14 east of Springville north of Hobbie Creek Canyon.



Fig. 7. Colony #32 near the mouth of Willow Creek Canyon southeast of Mona.



Fig. 8. Colonies #22A and #22 southeast of Mona on the Wasatch Mountains.



Fig. 9. Colony #8 southwest of Herriman on the north drainage of the Traverse Mountains.



Fig. 10. Clone #2, colony #1 and clone #3 in Harker's Canyon on the east drainage of the Oquirrh Mountains.



Fig. 11. Colony #5 in Coon Canyon southwest of Orr's Ranch on the east drainage of the Oquirrh Mountains.



Fig. 12. Colony #4 southwest of Magna on the east drainage of the Oquirrh Mountains.



Fig. 13. The dry, rocky habitat area northeast of Tooele on the west drainage of the Oquirrh Mountains.



Fig. 14. Clone #31, colony #16 and clone #17 in the same area (above), with leaves persistent in late November.



Fig. 15. The single isolated hybrid near the mouth of East Government Creek Canyon in the Sheeprock Mountains.



Fig. 16. Close up of clone #28 in mid-November.



Fig. 17. Colony #27 near Oak Creek Canyon on the west drainage of the Canyon Mountains.



Fig. 18. Clone #26 southwest of Kanosh on the west drainage of the Pahvant Mountains.



Fig. 19. Colony #30 east of Milford on the west drainage of the Mineral Mountains.



Fig. 20. Clone #29, the southern most relic hybrid on the west drainage of the Mineral Mountains.

DISTRIBUTION, LOCATION AND DESCRIPTION OF HYBRID CLONES

In the following discussion, the exact sites of all relic clones have been plotted on topographic maps and directions are derived from true north. Progressive distances are measured from the preceeding clone. Clones of largest area dimensions with small leathery spinulose-dentate leaves with 3-6 teeth per side, either green or bluish-green, persistent with color usually after mid-November, are considered F_1 generations because their characteristics are intermediate between those of the parents and the size of the clones indicates that they are older. Clones of smaller area dimensions with larger leaves of weaker texture, either bluntly toothed or lobed, shiny or dull, bluish-green or green, losing color and drying usually before late November, are considered backcrosses of either F_1 hybrids or later generation backcrosses to the Gambel oak parent, because their characteristics are intermediate between those of the adjacent F_1 clone and the surrounding Gambel oak and their smaller size indicates that they are younger. Descriptions will be based on these criteria unless mentioned otherwise.

The northern limit of relic hybrids is marked by clone #33 (101), on the Wasatch Mountains between Birch Creek and Beus Canyon, 1.8 miles southeast from Weber College in South Ogden, (2.9 miles north from the mouth of Weber Canyon). The growth, 20 x 15 x 12 feet is sheltered near large boulders on a southwest exposure at 5880 feet. Leaves are green in

summer, uniform oval 4.5 x 3.0 cm., spinulose-dentate with 3-5 large teeth per side; pubescence 2-8 rayed on the surface; 4-8 rayed, numerous 8 rayed beneath. One half of the leaves were green in early December. Large acorns were produced in 1957. Surrounding stumps indicate an old fire.

South 30 miles from clone #33, on a west exposure near the mouth of Dry Creek Canyon, 1.1 miles northeast from the University of Utah, (0.3 mile northeast from the Fort Douglas golf course clubhouse) clone #23 (67), 25 x 15 x 8 feet is growing at the periphery of a large circular colony of Gambel oak at 5250 feet. Leaves are uniform oval 7.5 x 4.5 cm., bluish-green, spinulose-dentate with 3-5 large teeth per side, retaining color until mid-November, some dry persistent until April. Pubescence 2-8 rayed above, mostly 4-6 rayed, and 1, 4-8 rayed, with many 4-6 rayed beneath. Numerous large acorns 2.9 x 1.5 cm. were produced in 1957, but squirrels harvested the entire crop. Stem galls are present.

South 1.3 miles, colony #21 (61) (62), 100 x 55 x 8 feet is growing on a south exposure 1.75 miles east of the University of Utah in George's Hollow (0.5 mile south from the mouth of Red Butte Canyon) at 5650 feet. The thicket is composed of two distinct clones; the upper portion (61), which is a probable backcross, 65 x 55 x 5 feet, and the lower F_1 portion (62), 55 x 35 x 8 feet. Leaves of (61) are shiny green above, pubescence 1, 2, 4-8 rayed, mostly 4 rayed; dull beneath, hairs 3-8 rayed, mostly 6-8 rayed; elliptical 7.5 x 3.5 cm.,

spinulose-dentate with 3-5 large teeth per side; gradually drying from mid-October to mid-November, completely shedding soon thereafter.

Leaves of (62) are bluish-green above, pubescence 1-7 rayed, mostly 4 rayed; yellow-green beneath, hairs 4-10 rayed, mostly 4 and 8 rayed; elliptical 4.5 x 2.0 cm., spinulose-dentate with 2-6 small teeth per side. They retain color after mid-November gradually drying, and persist to the following February. Past acorn production has been slight; none were produced in 1957.

Nine miles south (10.1 miles south-southeast from the University of Utah) near the mouth of Big Cottonwood Canyon, (0.8 mile northwest of the granite power plant) clone #24 (68) is growing on a southwest exposure at 5000 feet. Comprised of two nearly continuous thickets, it measures 50 x 25 x 10 feet. Leaves are dull bluish-green, broad oval 5.5 x 3.0 cm., not spinulose but with 3-5 sharp teeth per side; gradually drying on mature branches after mid-November and persistent until February, with leaves of vegetative sprouts retaining color. Pubescence 4-8 rayed above; mostly 6-8 rayed and very dense beneath. Many acorns 2.0 x 1.2 cm. were produced in 1954. Stem galls are present. Stumps within are the result of girdling by a porcupine. Oak bark constitutes a large percentage of this animal's diet in winter.

South 11 miles, colony #10 (21) (22), 175 x 160 x 8 feet is located on a south exposure of a side hill at 5700 feet,

(0.7 mile northeast from the mouth of Big Hollow) 1.9 miles northeast of Alpine. Leaves of the main scattered F_1 clone (21), are dull bluish-green, oval 6.0 x 3.5 cm., spinulose-dentate with 3-6 sharp teeth per side; pubescence 3-8 rayed above; 4-8 rayed mostly 8 rayed beneath. They retain color until mid-December, and gradually become dry. In 1954-55-56, this clone was parasitized by the midrib gall wasp Andricus reticulatus Bassett.²⁷ New foliage in 1957 was completely free of any new galls, although a few dry infested leaves from 1956 persisted. Past acorn production has been very slight. A few 2.4 x 1.5 cm. were produced in 1957 (plate 18).

Leaves of a small backcross (22), approximately 20 feet below the lower edge of the upper portion of (21) are shiny green above, pubescence 1-7 rayed; dull beneath, hairs 2, 4-7 rayed, predominately 4 rayed on both surfaces; oval 7.0 x 4.0 cm., slightly spinulose with 3-6 frequently double teeth per side, sinuses halfway to midrib; deciduous after mid-November.

At the mouth of Big Hollow, 0.7 mile southwest of colony #10, (1.2 miles northeast of Alpine) colony #11 (23, 24, 26, 28-35) is located on a south exposure at 5250 feet. The largest thicket is composed of two adjacent continuous, although distinctly different clones, with nine small clones scattered below.

Leaves of the lower west clone of the large clump, (23), a backcross, 40 x 35 x 10 feet are dull green, elliptical 5.0 x 2.0 cm. with 3-4 sharp teeth per side. They turn yellow

in mid-October and are deciduous before mid-November. Pubescence 2-10 rayed above; 4-10 rayed with many 8-10 rayed beneath. Stem and surface leaf galls are present. These galls, discussed in Part II, are common on Gambel oak and to a lesser extent on backcrosses expressing similar characters, but are present on only a few F₁ hybrids.

Leaves of the largest continuous upper east clone (24), the F₁ generation 95 x 40 x 12 feet, are shiny green above, pubescence 2, 4-6 rayed confined mostly to the midrib; dull beneath, hairs 1, 3 rayed on the midrib at the base; both surfaces nearly glabrous; small oval 4.0 x 2.3 cm., spinulose-dentate with 3-5 teeth per side; deciduous after mid-November. Many acorns were produced in previous years, but none were observed in 1957. Cups are conic-hemispheric, 1.0 cm. wide; shells are long pointed, length 2.4 cm. is greater than 2x the width, 1.0 cm. Stem and surface leaf galls are present. Many leaves of this clone were parasitized by the midrib gall wasp Andricus reticulatus in 1954-55-56. The adjoining west portion clone (23), during the same periods was only lightly parasitized. Foliage in 1957 was completely free of any new galls. Few infested dry leaves from 1956 persisted on both sections. The remaining smaller backcross clones are not parasitized by the midrib gall wasp, although stem and surface leaf galls are present. No acorns were observed on any during 1957 and with slight variation all are completely deciduous before mid-November.

Clone (26) 8 x 7 x 9 feet is 40 feet east from the upper end of (24). Leaves are shiny green above, pubescence 1-5 rayed confined to the midrib and larger veins; dull beneath, hairs 1-6 rayed mostly on larger veins; oval to obovate, 6.0 x 3.2 cm., with 2-6 large teeth per side.

Clone (28), 8 x 7 x 7 feet, 40 feet southeast from the upper end, and lower edge of (24), forms the distinct west portion of a slightly larger clump, with which it is continuous. Leaves are shiny green above, pubescence 4-6 rayed; hairs many, 4-8 rayed beneath; oval 4.6 x 2.7 cm., with 3-6 blunt teeth per side.

Clone (29), 12 x 12 x 10 feet forms the larger east portion. Leaves are shiny green above, pubescence 2, 4, 5 rayed; dull beneath, hairs 1-6 rayed, confined to the midrib on both surfaces; elliptical 7.0 x 3.0 cm., with 2-4 large blunt teeth per side.

Clone (30), 2 x 2 feet is approximately 10 feet north from the mid-section of (28) (29). Leaves are shiny green above, pubescence 4-7 rayed; dull beneath, hairs 1, 2, 4 rayed, confined to the midrib on both surfaces; elliptical 5.0 x 2.5 cm., with 5-6 deep frequently triple pointed teeth per side.

Clone (31), 3 x 3 feet, is 35 feet southeast from united clones (28) (29). Leaves are shiny green above, pubescence 1-6 rayed; dull beneath, hairs 1, 2, 4 rayed, confined to the midrib and larger veins on both surfaces; elliptical 4.5 x 2.7

cm., with 3-4 frequently deep double-tipped teeth per side.

Clone (32), 12 x 10 x 9 feet is located 40 feet southeast from the central lower edge of (24), midway between clones (25) and (31). Leaves are dull green, oval 6.3 x 3.6 cm. with 3-5 small blunt teeth per side. Pubescence mostly 4 rayed above; 1-6 rayed beneath, confined to the midrib and large veins on both surfaces.

Clone (33), 9 x 9 x 10 feet, is 15 feet southeast from united clones (28) (29), 20 feet northwest from clone (31). Leaves are shiny green above, pubescence 1, 2, 5 rayed; dull beneath, hairs 1-6 rayed, confined to the midrib and veins on both surfaces; elliptical-oval 6.5 x 3.7 cm., with 3-5 blunt teeth per side.

Clone (34), 3 x 3 feet is 16 feet southeast from the lower edge mid-section of (24). Leaves are shiny green above, pubescence 1-5 rayed; dull beneath, hairs 1-4 rayed, confined to the midrib and veins; elliptical 5.5 x 2.5 cm., with 3-5 large teeth per side.

Clone (35), 2 x 2 feet is approximately 10 feet northwest of (28) in line with the upper end of (24). Leaves are shiny yellow-green above, pubescence 1-5 rayed; pale green beneath, hairs 1-5 rayed, confined to the midrib and veins on both surfaces; elliptical 5.0 x 2.7 cm., spinulosa-dentate, with 3-5 short teeth per side.

Apparently clone (24), the F_1 generation, was a parent involved with Gambel oak to give rise to clone (23) initially.

Progressively later, the remaining younger clones grew from acorns, of clone (23) and (24) consorting freely with Gambel oak; possibly from self-fertilized acorns of (23) and (24); or from acorns of (23) and (24) backcrossed, since clones (23) and (24) produce the majority if not all the acorns today. Many of the smaller clones became established during the last century and represent backcrosses and possibly some F_2 and F_3 generations.

Between the second and third draw on the north side of Big Hollow, (0.3 mile north from colony #11) colony #11A (82) (81), is growing on a south exposure at 5500 feet. The main clone (82), measures 80 x 80 x 9 feet, with a small vegetative clone on the upper west edge. Leaves are shiny green above, pubescence 4-13 rayed; dull beneath, hairs 3-12 rayed, predominately 8 rayed throughout; elliptical 7.0 x 3.2 cm., spinulose-dentate with 3-6 large teeth per side; gradually deciduous after mid-November. Past acorn production has been very slight; none were produced in 1957. This clone appears to be a backcross.

The smaller dull green leaves of clone (81), similar to those of other F_1 hybrids, 8 x 8 x 9 feet, 15 feet below are elliptical 4.5 x 2.2 cm., spinulose-dentate, with 3-6 teeth per side, and gradually deciduous after early December. Pubescence 4-10 rayed on the surface; 1, 4-14 rayed, mostly 8-9 rayed beneath. Few acorns were produced in 1957.

South 5.5 miles, 4.5 miles south-southeast of Alpine, clone #12 (36), 65 x 65 x 12 feet is located on a southwest exposure of Mahogany Mountain at 5460 feet, (2.5 miles south of American Fork Canyon). Leaves on straggly branches are leathery, bluish-green above, pubescence 2-8 rayed; yellow-green beneath, hairs 1, 4-8 rayed; variable in size, usually elliptical to oval, 6.5 x 3.5 cm. to 10.5 x 5.7 cm., spinulose-dentate, with 3-5 teeth per side; gradually drying after mid-November, persistent until January. Few acorns 3.0 x 1.6 cm. were present in litter, but none were produced in 1957 (plate 18). Stem galls are present.

South 4.8 miles, 1.5 miles east of Lindon, (2.3 miles northwest from the mouth of Provo Canyon) colony #13 (37)-(39), (41), (42), is located on a southwest exposure below the mouth of Sumac Hollow, at 5020 feet. The central F₁ clone (38), measures 70 x 65 x 15 feet; leaves are bluish-green, elliptical 6.5 x 3.5 cm., spinulose-dentate with 2-5 large teeth per side; mostly deciduous by early December. Pubescence 2, 4, 6, 8 rayed on the surface; 1-8 rayed beneath. Acorn production has been good; numerous shells broad-oval 1.7 cm. long with hemispheric cups 1.5 cm. wide were frequently encountered. Two small seedlings from acorns produced in 1953, with leaves similar to those described above, and with the acorn shell attached, were observed within the clone in 1954, indicating this clone to be probably self-fertile. Many cups were present from 1956; no acorns were produced in 1957.

Clone (37), a backcross, is continuous on the east side near a fence and resembles Gambel oak. Leaves are green, oval 8.0 x 5.0 cm., with 3-4 large, blunt and spinulose tipped lobes per side; deciduous before mid-November; pubescence sparse 1-8 rayed on the surface; numerous 1-8 rayed beneath.

Clone (39), a single small growth 10 feet south of (38), possibly of vegetative origin, exhibits variable dimorphic leaves. Generally they are bluish-green above, pubescence 1-8 rayed; yellow-green beneath, hairs 1-8 rayed, mostly 4 rayed throughout; oval 5.0 x 3.0 cm., spinulose-dentate with 3-5 teeth per side. Some deeply lobed leaves of weaker texture were curled and copper-brown color from the cold by early December, while others of the original description retained color. Rarely do leaves of these hybrids and backcrosses become copper-brown; they are usually light tan color when dry.

Clone (41), a small probable backcross, is north of clone (37) near the fence. Leaves are bluish-green above, pubescence 4-8 rayed, mostly 4 rayed; yellow-green beneath, hairs 4-8 rayed, many 5-6 rayed; elliptical 5.0 x 2.5 cm., with narrow bases, and 3-6 often double teeth per side; deciduous in early November.

A small clone (42), possibly of vegetative origin is east of the fence and clone (37). Leaves are dull green with 1-8 rayed pubescence on both surfaces, more numerous beneath; oval 7.0 x 4.5 cm., with 3-4 large spinulose teeth per side.

A hybrid clone was recently found by Dr. Earl M. Christensen one mile southeast from colony #13 at approximately 5400 feet elevation; and another 5.6 miles south at about 5000 feet, 2 miles east from the north end of Provo City. A single hybrid clone discovered in 1955 at 830 East 1430 North Street at 4600 feet in Provo, was removed by excavation and a building now exists on the site. A specimen was collected however; leaves, are dull green; pubescence 1-8 rayed on both surfaces; obovate 5.5 x 3.7 cm., spinulose-dentate with 4-5 frequently double teeth per side.

Colony #14 (43)-(46), thirteen miles south from colony #13, consists of three scattered clones. It is located on a southwest exposure at 5650 feet, 1.5 miles east of Springville, (1.3 miles northwest from the mouth of Hobbie Creek Canyon). Clone (44) a large probable F_1 generation, measures 35 x 30 x 15 feet; leaves are bluish-green above, pubescence dense 1, 5, 8-10 rayed; bluish-green beneath, stellate hairs dense 8-16 rayed; small elliptical 4.5 x 2.5 cm. with 3-4 small deep blunt teeth per side; gradually deciduous after early December. Past acorn production has been moderate. Cups are conic-hemispheric 1.0 cm. wide with long, oval pointed shells, length, 2.2 cm. exceeds 2x the width 1.0 cm. (plate 18). No acorns were produced in 1957. A ring count of one large stump within shows an age of 90 years when burned by fire; surrounding larger branches survived, but date of the fire is not known.

Clone (43) growing nearly continuous with the northeastern edge of (44) shows only slight hybrid influence. Leaves are dark shiny green above; pubescence 1-9 rayed; yellow-green beneath, hairs 1-8 rayed predominately 4 rayed; obovate 7.0 x 5.2 cm. with 3-4 deep, frequently obovate lobes per side. Its deciduous and fruiting habits are not known. This specimen is best referred to as "introgressed Q. gambelii," rather than a backcross.

Clone (45), a backcross, 8 x 10 x 8 feet is 30 feet north above. Leaves similar to those of Gambel oak, are shiny green above, pubescence 1-11 rayed; pale green beneath, hairs 4-15 rayed; elliptical 7.0 x 3.5 cm., with 3-5 deep lobes per side; gradually deciduous after mid-November, some leaves pale green in early December. Acorn production has been slight; many, oval 1.9 x 1.1 cm. were produced in 1957 (plate 18). Stem galls are present.

Clone (46), a possible backcross, 8 x 8 x 8 feet, 100 feet west of (44) is nearly obscured by Gambel oak. Leaves are shiny green above, pubescence 2-8 rayed; pale green beneath, hairs 3-8 rayed; elliptical 6.0 x 3.2 cm., with 3-5 small deep lobes per side; gradually deciduous after early December. Acorn production has been slight; many, long oval, 2.5 x 1.2 cm. were produced in 1957 (plate 18). An adult female Nut Weevil, Curculio strictus Casey, was observed with its beak firmly imbedded inside an acorn shell. Their restrictive effect prohibiting acorn germination will be discussed later.

Twenty-six miles southwest, clone #36 (104), 25 x 25 x 10 feet is growing among limestone cliffs at 6700 feet on the south exposure of Bear Canyon (0.3 mile from the mouth), 2.7 miles east-northeast of Mona. Leaves with 1-8 rayed pubescence on both surfaces are elliptical, 5.2 x 2.2 cm., spinulose-dentate with 3-6 teeth per side, gradually deciduous after late November. Past acorn production has been slight if any.

Southwest 0.75 mile, (2.2 miles east of Mona) clone #35 (103), a backcross, 50 x 40 x 10 feet is growing on a southwest exposure near limestone outcrops on the south side near the mouth of Dry Canyon at 5950 feet. Leaves are shiny green above, pubescence 1, 4-11 rayed; 1-9 rayed beneath; elliptical 10.0 x 3.8 cm., coarsely spinulose-dentate with 4-6 large teeth per side; gradually deciduous after late November. Past acorn production has been slight.

South 2 miles, on a west exposure, (0.2 mile south from the mouth of Willow Creek Canyon) 2.2 miles southeast of Mona at 5560 feet, approximately 20 distinct clones covering an area 80 x 100 yards comprise colony #32 (90)-(100). Specimens were collected from eleven clones which retained some leaves in early December. Acorn production could not be determined at this date. The largest F₁ generation is located centrally with younger backcross clones completely encircling it on all sides, and Gambel oak in turn surrounding the entire colony, illustrating a classic example of hybridization under natural conditions. Taxonomic identification of some backcrosses would

elliptical 8.5 x 4.7 cm. with 3-5 blunt teeth per side; pubescence 2, 4-8 rayed above; 1, 3-8 rayed beneath. A hybrid clone exists 60 feet east and another approximately 20 feet south of (94); both clones retained some pale green leaves.

Clone (95), 30 x 27 x 12 feet, 70 feet southeast of (94) retained some large pale green leaves, broad-oval to obovate, 10.0 x 6.7 cm. with 3-5 large shallow lobes per side; pubescence 2-12 rayed, frequently 8 rayed above; hairs numerous 1-8 rayed beneath.

Beginning 80 feet southwest, four small hybrid clones with very few dry leaves are scattered for 40 feet, descending west. Clone (96), 5 x 5 x 8 feet is an additional 50 feet below. Leaves, dry persistent, are elliptical to broad-oval 7.5 x 5.5 cm. with 3-4 lobes per side; pubescence 1-6 rayed, mostly 1-4 rayed on both surfaces.

Directly below, clone (97), 27 x 27 x 12 feet retained many slightly green shiny leaves elliptical 9.0 x 4.5 cm., with 4-5 large shallow teeth per side; pubescence 2-9 rayed above; 1-8 rayed beneath, mostly 2-4 rayed throughout.

Clone (98), 30 x 30 x 12 feet, 10 feet north retained the majority of pale green leaves. They are elliptical 8.6 x 3.5 cm. with 3-6 deep, slender, slightly blunt teeth per side; pubescence 2-9 rayed above; 1-8 rayed, mostly 5-6 rayed beneath.

North 30 feet, clone (99) 125 x 100 x 4 feet retained all green leaves on short extremely rigid branches, which apparently have been heavily browsed by deer during past winters.

Leaves are elliptical 5.8 x 3.4 cm., spinulose-dentate with 4-6 teeth per side; pubescence 2-10 rayed above; 1-12 rayed beneath, 10-12 rayed near the base. A hybrid clone with dry leaves southwest, and two additional adjacent clones northwest of (99) complete the total which were not collected.

Clone (100), 30 x 30 x 16 feet, north of clone (99) retained many dry leaves, elliptical 7.6 x 4.0 cm., spinulose-dentate with 4-6 large deep teeth per side; pubescence sparse 2-8 rayed above; dense 1-8 rayed beneath.

Similar to the hybrid swarm of colony #11, these clones are considerably older and contain a greater proportion of the evergreen character, persisting green or moderately so for one month longer. The F_1 clones throughout their distribution in the Great Basin are generally distinguishable and exert "individual" characters upon the various backcross types, even though variability may exist within the leaf morphology and deciduous habits of Gambel oak. Rarely can green leaves be observed on Gambel oak after 7 November, although excess parasitism with galls on the leaf surfaces, physical disturbance of roots (excavation) and direct access to underground or surface water may prolong the drying and deciduous process.

Southwest 0.75 mile, colony #22A (83) (84), 40 x 30 x 8 feet is growing on the west-facing bench between Wildcat Gulch and Wide Canyon, (2.3 miles southeast of Mona) at 5350 feet. Leaves of the large clone (84), are shiny green above, dull beneath, pubescence 1-7 rayed on both surfaces; elliptical

9.5 x 5.0 cm., spinulose-dentate with 3-5 large teeth per side; gradually deciduous after late November. Acorn production has been slight, if any.

One-hundred feet east, clone (83), a backcross 10 x 8 x 8 feet retained a few dry leaves in early December. They are oval 9.2 x 6.5 cm. with 3-4 variable deep and shallow lobes per side; pubescence sparse 1-8 rayed above; numerous 1-8 rayed beneath. Acorn production has been slight. Both clones have surface leaf galls and have been heavily browsed.

Southeast 0.35 mile, colony #22 (63)-(66), is growing on a west exposure between Long and Wide Canyon at 5650 feet, (2.7 miles southeast of Mona). Leaves of the F₁ generation clone (63), 75 x 50 x 12 feet are bluish-green, leathery, elliptical 8.5 x 4.5 cm., spinulose-dentate with 3-5 shallow teeth per side; gradually drying after mid-December, persistent until February. Pubescence sparse 1, 4 rayed above, confined to the midrib and veins; dense, 1-6 rayed beneath. Acorn production has been slight. Lower branches are heavily browsed. Palatability of these hybrids cannot be concluded from the previous examples because deer have been concentrated in this winter range area.

The four remaining clones represent backcrosses. Leaves of clone (66), south adjacent to the lower part of (63) are shiny-green above, pubescence sparse 1-4, 6, 8 rayed; 1-8 rayed beneath; elliptical, 10.0 x 5.7 cm. with 3-5 shallow lobes per side; drying after early November, persistent to late December.

Leaves of clone (65), south adjacent and above (66) are shiny green above, pubescence 1-4 rayed; 1-7 rayed beneath; elliptical, with narrow bases, 7.0 x 3.0 cm. with 3-4 small shallow lobes per side; deciduous after early November. Directly below (west) another backcross clone retained dry leaves in late November.

Leaves of clone (64), south and above (65) are shiny bluish-green above, pubescence 1-5 rayed on both surfaces, sparse above; oval 8.0 x 4.8 cm., with 4-6 large teeth per side; drying after mid-November, persistent until mid-December.

On the north drainage of the Traverse Mountains 16 miles southwest of Salt Lake City, clone #9 (20), 120 x 50 x 8 feet is growing in a wash on a gentle northeast exposure at 5400 feet, approximately 2.0 miles southwest of Herriman, (0.65 mile east-northeast from colony #8). Leaves are dull green, elliptical 7.2 x 3.8 cm., spinulose-dentate with 3-5 teeth per side; pubescence 1-8 rayed on both surfaces; gradually deciduous after mid-November; vegetative sprouts green in early December showed cropping by cottontails. Acorn shells 2.0 x 1.4 cm., with cups 1.7 cm. wide were present in the litter (plate 18). Past production has been slight; none were produced in 1957. Stem galls are present.

Colony #8, (16)-(19), (80), 0.65 mile west-southwest of clone #9 is growing on a gentle northwest exposure near the mouth of Indian Hollow at 5400 feet, (200 feet west of a large brown boulder) 2.35 miles southwest of Herriman. Small clones,

apparent backcrosses surround the central F_1 hybrid. The F_1 clone, (19) measures 16 x 13 x 8 feet. Leaves are elliptical 5.2 x 2.2 cm., bluish-green above, green beneath, pubescence 1-8 rayed; spinulose-dentate with 3-6 teeth per side; gradually deciduous after mid-November. Acorn cups 1.5 cm. wide and shells 1.7 x 1.3 cm. were sparse in the litter.

Clone (18), 3 x 3 feet is 10 feet southwest on the west bank of a wash. Leaves are shiny green above, pubescence sparse 1-4, 5, 8 rayed; hairs 1-8 rayed beneath; elliptical 5.0 x 2.4 cm., repand with 3-5 short frequently blunt teeth per side; deciduous after mid-October.

Clone (16), 3 x 3 feet is 10 feet southwest of (18) on the bank of the wash. Leaves of the larger main growth are bluish-green above, pubescence sparse 1-8 rayed; pale green beneath, hairs 1-8 rayed; oval to obovate 7.8 x 4.6 cm., repand with 3-4 short blunt teeth or lobes per side; deciduous in mid-October. Leaves on a few small branches within, are green elliptical, 4.5 x 2.2 cm. with 3-5 short blunt teeth per side; dry persistent prior to mid-October. Pubescence sparse 2, 4 rayed above; 1-8 rayed beneath.

Clone (17), 3 x 2 feet is across the wash 15 feet northwest from (19). Leaves are shiny green above, pubescence sparse 2-4 rayed; green beneath, hairs 1-6 rayed; elliptical, 5.5 x 3.2 cm. with 3-5 deep teeth per side; deciduous in late October.

Leaves of clone (80), 3 x 3 x 3 feet, 30 feet east of (19) are shiny green above, pubescence sparse 1-6 rayed; dull beneath,

hairs 1-8 rayed; elliptical 5.7 x 3.3 cm. with 3-5 small lobes per side; deciduous in late October. Clone #9 and colony #8 indicate an old fire burn.

On the east drainage of the Oquirrh Mountains, 4.5 miles northwest, clone #7 (15), 25 x 20 x 8 feet is located on a south exposure in Keystone Gulch at 6360 feet, (1.3 miles west-northwest from Lark). Leaves are bluish-green on both surfaces, elliptical 4.8 x 1.9 cm., spinulose-dentate with 3-4 teeth per side; gradually deciduous after mid-November. Pubescence 4-10 rayed above; 1, 4-12 rayed beneath, numerous 6-8 rayed. Many acorns 2.0 x 1.1 cm. were produced in 1954 (plate 18); production was sparse in 1957.

North 6.3 miles, clone #2 (3), 80 x 50 x 7 feet is growing on a south-facing slope in Harker's Canyon at 5640 feet, (3.0 miles south-southwest from the Bacchus powder plant) 5.5 miles south of Magna. Leaves of this dense thicket are dull bluish-green above, pubescence 2, 4-8 rayed; pale green beneath, hairs 1, 4-10 rayed; elliptical 4.8 x 1.9 cm., leathery spinulose-dentate with 3-4 small teeth per side; gradually deciduous in late October, dry persistent until late January. Past acorn production has been slight if any. Vegetative sprouts exhibit cropping by cottontails.

West 0.5 mile, colony #1 (2) (1), 80 x 60 x 10 feet is growing on a south exposure near the canyon bottom at 5760 feet. Leaves of the large dense clone (2), are dull bluish-green, elliptical 4.3 x 2.4 cm., leathery spinulose-dentate with 3-5

deep teeth per side; gradually drying after mid-December, persisting partially green until late January, with a few remaining green in March. Leaves on young vegetative growth are evergreen. Pubescence 1, 3-8 rayed above; 1, 4-8 rayed beneath. This is the only clone on the Oquirrh Mountains parasitized by the midrib gall wasp A. reticulatus. In 1954 more than 150 of these small, one quarter inch round, dark brown galls, which form in the midrib near the leaf base, were observed on leaves of many branches less than 2 feet long. This parasitism was present in 1955-56 also, but in 1957 identical to clones (21) (23) and (24) near Alpine, new leaves were completely free of any midrib galls. Some dry infested leaves from 1956 persisted. Although many thousands of galls may be found on leaves of a single tree only infrequently is it possible to determine that any real damage has been done. Scrub oak can also withstand the incidental damage done by most Cynipidae.¹⁶

These wasp populations are isolated because they are strictly limited to a single species or at most to a small group of closely related oaks, which are more abundant in the mid and southern latitudes of Arizona and New Mexico. They cannot spread readily unless a continuous host flora is available. They are further restricted by an extremely short life span, susceptibility to sudden climatic changes, and weak flight ability.^{17, 6} (Discussed in Part II)

No fully developed acorns have been found, although a few 1.6 x 0.9 cm. were produced in 1957 (plate 18). In 1954 three seedlings were observed within clone (2). Leaves of these young plants with the acorn shell attached, were similar to those of clone (2). Their location, size and morphology indicate that they grew from acorns produced by this clone in 1953. Clone (2) and (38) are the only two known to have produced viable, probably self-pollinated acorns which germinated under natural conditions. Burned stumps show ages of 45, 69, 79, 83, and 87 years. Only one branch approximately 118 years old with 34 annual rings since the fire, survived, indicating that the fire occurred about 1920.

Leaves of clone (1), 5 x 5 feet, a backcross 20 feet east from the lower edge of clone (2), are light shiny green above, pubescence 2-8 rayed, mostly 4 rayed on both surfaces; elliptical 7.0 x 3.2 cm. with 3-5 frequently deep large teeth per side; gradually drying after early November; persistent until early December. Past acorn production has been slight. Many 2.3 x 1.6 cm. were produced in 1957 (plate 18).

Clone #3 (4), 16 x 12 x 7 feet, 0.2 mile west is growing beside a large limestone outcrop on the south-facing slope at 6000 feet. Leaves are dark shiny green above, pubescence 3-8 rayed; light green beneath, hairs 1, 4-8 rayed, many 8 rayed; elliptical 5.0 x 2.5 cm., spinulose-dentate with 3-5 teeth per side; drying in November, persistent until late December. Past acorn production has been slight, but many, 2.3 x 1.2 cm. were

produced in 1957, (plate 18).

North 1.8 miles in Coon Canyon, colony #5 (10) (11), is growing among limestone outcrops on the south exposure of the canyon bottom near the creek at 5300 feet, 2.25 miles southwest of Orr's Ranch, (which is 2.0 miles south of Magna). Leaves of the largest clone (10), a possible backcross 250 x 150 x 12 feet, with young expanding growths scattered higher among the rocks, are bluish-green, elliptical 4.7 x 2.0 cm., spinulose-dentate with 4-5 teeth per side; drying in mid-November with shades of red and yellow in leaves of older branches and the combination red and green in young vegetative growth; persistent until early December. Pubescence 1-8 rayed on both surfaces. In 1957 an estimated 7000 acorns 2.4 x 1.3 cm. were produced, many of which were potentially viable (plate 18). Initially the greatest environmental pressure can be observed with this example. The majority of these acorns, and nearly all others including those of Gambel oak are parasitized by larvae of the Nut and Acorn Weevil and the Catalina Cherry Moth. Considerable production has been noted in previous years (1954), but not a single seedling has been observed. (Discussed in Part II)

A specimen from this clone was collected June 16, 1915 by A. O. Garrett. The leaves are similar with the exception of size, 2-4.0 x 1.5-2.0 cm. Garrett commented that Dr. Rydberg said, "It looks like Quercus venustula", which is fairly common in northern New Mexico and extends into southern Colorado in the

Raton Mountains. However, specimens collected by the author near Raton Pass, Colfax County in northern New Mexico, and Phantom Canyon in Fremont County in south-central Colorado in 1956 were identified as Quercus undulata Torr. by Dr. Tucker, who noted that one specimen possibly contained some Q. turbinella influence. Near Phantom Canyon he found two slightly atypical shrubs of Q. turbinella and comments that "typical Q. gambelii was abundant on the opposite side of the canyon". Specimens of two isolated clones growing on the southwest exposure of a wash near Penrose, Fremont County, Colorado fairly green in mid-November, were identified as Q. gambelii Nutt., possibly introgressed with Q. grisea Liebm.

Across the creek, about 50 feet south from the west end of (10), clone (11), 5 x 4 x 8 feet is growing beneath the branches of a Gambel oak. Leaves are very small, leathery, bluish-green, ovate wide at the base 2.5 x 1.5 cm., sharp spinulose-dentate with 4-5 deep frequently double and triple pointed teeth per side; drying and gradually deciduous after mid-November. Pubescence dense 4-14 rayed, many 8-12 rayed above; more dense beneath, hairs 5-14 rayed, mostly 8-12 rayed. Many acorns 2.6 x 1.1 cm. (shell length greater than 2X the width) were produced in 1957 (plate 18). Stellate pubescence is also prominent on the apex of the fruit shells and on young branches. This clone does not appear to be a backcross.

Colony #6 (12)-(14), 58 x 58 x 6 feet is located on the west exposure of the first large draw west, 0.4 mile northwest

from colony #5, at 5600 feet. Leaves of the main F_1 clone (12), are noticeably uniform, bluish-green, elliptical 5.3 x 2.3 cm., spinulose-dentate with 4-5 teeth per side; drying in early November and persisting for a month longer; pubescence 1-8 rayed, but sparse on the upper surface. Numerous acorns were produced in 1954; none were produced in 1957. Charred stumps within indicate an old fire burn.

Leaves of clone (13), a backcross, 4 x 4 x 4 feet growing on the lower north edge of (12) are shiny green above, pubescence sparse 1, 2, 4 rayed; dull beneath, hairs 1, 2, 4-6 rayed, with very few 5, 6 rayed; elliptical 7.0 x 3.5 cm. with 4-5 slightly blunt shallow teeth per side.

Clone (14) 8 x 5 x 5 feet nearly identical to (13), is adjacent to the lower south edge of (12). Leaves are shiny green above, pubescence 1-4 rayed; dull beneath, hairs 1-4 rayed with very few 5 rayed. Stem galls are present throughout the colony.

The northern most colony on the Oquirrh Mountains #4 (5)-(9), is growing on the south exposure of a large draw at 5700 feet, 1.45 miles west of Orr's Ranch. Leaves of the main F_1 clone (5), 100 x 50 x 5 feet are bluish-green, elliptical 5.5 x 2.8 cm., spinulose-dentate with 4-5 frequently deep teeth per side; pubescence sparse 4-10 rayed above, mostly 8 rayed; 1, 4-14 rayed beneath, numerous 8-10 rayed; gradually deciduous after mid-November. Few large acorns 2.9 x 1.6 cm. were produced in 1957 (plate 18). Burned stumps 50 years old within indicate an old fire.

Clone (8), 8 x 6 x 5 feet is growing 40 feet below the south end of (5). Leaves are bluish-green, elliptical 5.5 x 2.3 cm., spinulose-dentate with 3-5 teeth per side; gradually deciduous after mid-November. Pubescence 1-8 rayed above; 1-14 rayed, mostly 8-10 rayed beneath. Few if any acorns were ever produced.

A small young clone (6), 2 x 2 feet, 40 feet below the central part of (5) is noticeably different. Leaves in mid-November are leathery bluish-green, very small oval, 2.7 x 2.0 cm., wide at the base, sharp spinulose-dentate with 4-5 frequently double teeth per side. This clone does not appear to be a backcross.

Among rock ledges 40 feet below, clone (7) a backcross, 3 x 3 feet exhibits dimorphic foliage characters similar to clone (39) east of Lindon on the Wasatch Mountains. In 1954 leaves on several branches were similar to those of (6) above, retaining full color in mid-November. Others, however, 4-8 cm. long, obovate, shiny green above, and deeply lobed were drying; some were yellow, and others were already shed. In 1957 leaves which resembled this latter type were collected. They are shiny, bluish-green above, pubescence sparse 1-8 rayed above; numerous 1-8 rayed beneath; elliptical 7.8 x 4.4 cm. with 4-5 frequently double-pointed lobes per side.

Clone (9) a backcross, 3 x 3 feet, north of clone (7) exhibits slight hybrid characters. Leaves are bluish-green, obovate 5.0 x 3.0 cm. with 4-5 frequently double-pointed lobes

per side; pubescence sparse 1-6 rayed above; sparse 1-8 rayed beneath, with higher ray numbers 5-8, near the midrib. This specimen may also be considered "introgressed Q. gambelii".

On the west drainage of the mountains northeast of the Tooele Smelter, which is 3.5 miles northeast of Tooele, eight scattered clones and colonies are growing in an area of numerous limestone outcrops. Generally exposed to the southwest, this area receives a majority of direct sunshine during the warmest periods each day. Colony #15 (47) (48), is located on a southwest exposure in the first large draw north from the mouth of Flood Canyon at 5600 feet, (2.85 miles north of the Tooele Smelter). Leaves of the F_1 clone (47), 135 x 55 x 8 feet scattered in its extent, are bluish-green, oval 4.0 x 2.7 cm., spinulose-dentate with 3-4 teeth per side; sinuses are obtuse. Pubescence 1-8 rayed with 7, 8 rayed sparse on veins on the surface; 4-8 rayed with many 7-8 rayed beneath; gradually drying in mid-December; many persistent until mid-February. Past acorn production has been slight if any.

Clone (48), a backcross 20 feet west from the upper part of (47) retained only a few dry leaves in late December. In summer they are shiny green above, pubescence 1-6 rayed; dull beneath, hairs 1-8 rayed, mostly 4-6 rayed; elliptical 5.2 x 2.5 cm., spinulose-dentate with 4-5 teeth per side; drying after early November. Several acorns 2.6 x 1.4 cm. were produced in 1957 (plate 18). Stem galls are present on this clone, but none were observed on the F_1 hybrid, (47).

South 1.2 miles, colony #16 (49) (50), is located on a southwest exposure at 5650 feet on the north side near the mouth of the first large draw south of Flood Canyon, (1.9 miles north of the smelter). Leaves of the F₁ clone (49), 30 x 20 x 7 feet are shiny bluish-green above, pubescence 3-8 rayed; dull beneath, hairs 1-10 rayed with many 8 rayed beneath; elliptical 4.7 x 2.5 cm., spinulose-dentate, with 3-4 teeth per side, spines pronounced 2 mm. long; sinuses shallow obtuse; gradually deciduous after mid-November, nearly all leaves shed by late December. Past acorn production has been good, but none were produced in 1957.

Leaves of a backcross clone (50), 25 feet east above (49) are of weaker texture, shiny green above, pubescence 1-8 rayed mostly 3-6 rayed; dull beneath, hairs 1-8 rayed; elliptical 6.7 x 3.2 cm., spinulose-dentate with 2-4 shallow teeth per side; sinuses are obtuse. Acorn production has been slight if any.

A single tree form #31 (89), a possible backcross, with surface leaf galls, is growing on a gentle southwest exposure near a wash, (0.5 mile west-southwest of colony #16) at 5060 feet. The tree is ten feet high and trunk diameter is 8 inches near the base. Leaves are green, elliptical 6.8 x 3.0 cm. with 3-4 large deep teeth per side; sinuses are acute; gradually deciduous after early December. Pubescence 1-16 rayed mostly 8-10 rayed above; dense 1-16 rayed with many 8, 13-16 rayed beneath. Many acorns 2.4 x 1.6 cm. were produced in 1956 and 1957 (plate 18). The endosperm within all shells had been eaten

by the parasitic insect larvae, another example of their destructive effects. This tree survived a fire which ravaged the area after the turn of the century. Remaining hybrid stumps nearby indicate a fate possibly followed by many young clones, accounting somewhat for their sparsity and size, since regrowth after fires limits the expansion of many clones.

Clone #17 (51), 60 x 35 x 8 feet is growing at 5900 feet on a northwest exposure, in the first large draw south of Flood Canyon, 0.3 mile east of colony #16. Leaves are leathery bluish-green, elliptical 6.8 x 3.2 cm., spinulose-dentate with 4-5 teeth per side, sinuses are obtuse; pubescence 5-10 rayed above; 1, 4-10 rayed, mostly 6-8 rayed beneath. The majority of leaves retain color in late December and are dry persistent in late January. Many acorns 2.6 x 1.5 cm. were produced in 1957; past production has been moderate (plate 18).

Clone #18 (52), 20 x 10 x 6 feet is growing at 6900 feet (highest elevation) on a south exposure among huge limestone outcrops at the head of the first draw 0.6 mile northeast of clone #17. Leaves are shiny green above, pubescence 2-8 rayed, mostly 4, 5 rayed; 1-8 rayed, mostly 8 rayed beneath; small elliptical 3.8 x 1.8 cm. with 3-4 deep teeth per side; gradually drying after mid-November, persistent until late January. Vegetative sprouts are green in late December. Few acorns 2.0 x 1.2 cm. were produced in 1957 (plate 18).

Southeast 0.5 mile from the mouth of this canyon the two largest clones of colony #19 (53) (54), are growing at 5600 feet.

They are located on a southwest exposure at the mouth of the first large draw northwest from the mouth of Pass Canyon, (1.4 miles north of the smelter). Leaves of F₁ clone (53), 15 x 15 x 10 feet are green, elliptical to oval, 4.5 x 2.8 cm., spinulose-dentate with 4-5 teeth per side; gradually deciduous after early December, partially green in late January; pubescence 2, 4-10 rayed above; 1, 3-12 rayed, mostly 8 rayed beneath. Bark is silver-gray. Many acorns 2.2 x 1.3 cm. were produced in 1954 and 1957 (plate 18).

Leaves of clone (54), a backcross 12 x 12 x 12 feet, 20 feet north are shiny green above, pubescence 2-10 rayed; 2-8 rayed, mostly 8 rayed beneath; elliptical 6.3 x 3.0 cm. with 3-4 large deep teeth per side; gradually drying in late October and completely deciduous in January. Many acorns 2.0 x 1.1 cm. were produced in 1957 (plate 18).

Scattered west below, in and near a wash, are six smaller clones (55)-(59), at approximately 5500 feet elevation. Leaves of clone (55), 15 x 12 x 4 feet, a probable backcross approximately 100 yards below (53) are green, variable, usually elliptical 6.2 x 2.8 cm. with 3-6 deep, frequently double and triple pointed teeth per side; gradually fading after late October, dry persistent in early November. Pubescence sparse 1-6 rayed above; numerous 1-6 rayed beneath, predominately 4 rayed on both surfaces.

Leaves of clone (56), a probable backcross approximately 50 yards below (55) are bluish-green, variable, usually elliptical

to oval, 4.7 x 3.0 cm. with 3-5 frequently double pointed lobes per side; sinuses variable, acute-deep, others shallow-obtuse. Pubescence dense on both surfaces, 2-10 rayed above; 2-10 rayed, mostly 6-8 rayed beneath; retaining color in early November, gradually drying and persistent through December. A single clone with similar characters is growing on a side hill a short distance south of this clone, across the wash.

Leaves of clone #19A (57), a F_1 generation, approximately 50 yards below (56) are bluish-green, uniform oval 5.5 x 3.0 cm., spinulose-dentate with 4-6 frequently double teeth per side; gradually deciduous after late November. Pubescence 2, 4-8 rayed above; 1-8 rayed beneath, mostly 8 rayed on both surfaces. Few acorns 2.3 x 1.2 cm. with cups 1.6 cm. wide were produced in 1957 (plate 18).

Leaves of clone #19B (58), a F_1 generation west of (57) are bluish-green, oval 4.8 x 3.3 cm., spinulose-dentate with 4-5 deep frequently double teeth per side; gradually deciduous after late November. Pubescence 2-8 rayed above; 1, 4-8 rayed beneath, mostly 8 rayed on both surfaces. Few acorns 2.2 x 0.9 cm. with cups 1.2 cm. wide were produced in 1957 (plate 18).

Leaves of clone (59), a probable F_1 generation, west of (58) are bluish-green variable, usually elliptical 5.7 x 3.0 cm. with 5-6 teeth per side; sinuses variable, deep and shallow; gradually deciduous after early November; pubescence 1-8 rayed on both surfaces, mostly 4, 5 rayed, dense on the lower surface.

Clone #20 (60), 25 x 20 x 12 feet is growing on a south exposure at 5850 feet in the first large draw 0.2 mile east from colony #19 in Pass Canyon. Leaves are bluish-green elliptical 5.0 x 2.8 cm., spinulose-dentate with 3-4 teeth per side; gradually drying and deciduous after mid-December; pubescence 1-8 rayed on both surfaces. Many acorns 1.8 x 1.2 cm. were produced in 1957; past production has been moderate (plate 18). Stem galls are present.

The mystery surrounding the establishment of Gambel oak on the Sheeprock Mountains, an isolated stand southwest of Vernon, is most perplexing. Christensen⁸ questioned whether it is a relic of a once continuous tongue from the Canyon Mountains north via the Gilson, and the East, North, and West Tintic Mountains where Gambel oak is apparently completely lacking today, or a southward migration from the Oquirrh Mountains via the North Tintics or both; the opposing theory linking man, birds, or rodents as agents of dissemination. The presence of a single small hybrid clone on the Sheeprock Mountains in a habitat typical of other relic hybrids in the Great Basin, confirms the relic theory, but what can account for the absence of any oak on any immediate or connecting mountain ranges to the east, west, north and south of the Sheeprocks today?

This isolated stand is separated from the southern limits of Gambel oak on the Oquirrh Mountains by a distance of 25 miles. The hybrid on the Sheeprocks is separated from those on the

Oquirrh and Wasatch Mountains by a distance of 40 miles and from the single colony south on the Canyon Mountains by a distance of 50 miles. Clone #28 (85), 8 x 7 x 8 feet is growing on a south exposure at 6400 feet, in the first large draw north from the mouth of East Government Creek Canyon, (approximately 12.0 miles southwest of Vernon). Leaves are bluish-green, elliptical 4.6 x 1.9 cm., spinulose-dentate with 3-4 small teeth per side; sinuses are obtuse; drying in early November and gradually deciduous through December; pubescence 1-8 rayed on both surfaces. It is probable that acorns were never produced. Stem and surface leaf galls are present.

The only hybrid known to exist on the Canyon Mountains was discovered by W. Leslie Robinette. Colony #27 (72)-(76), is located on a west exposure at 6000 feet, at the bottom of the largest rockslide, in the first hollow draw north from the mouth of Oak Creek Canyon, (3.0 miles east-southeast from Oak City). Leaves of the largest upper F_1 clone (75), 40 x 35 x 7 feet are bluish-green above, yellow-green beneath, oval 4.3 x 2.3 cm. with 4-5 teeth per side; sinuses are very shallow, repand; becoming dry in late October, and gradually deciduous, some dry persistent until April; pubescence 1-8 rayed throughout on both surfaces.

Leaves of clone (74), a backcross 2 x 2 feet, approximately 5 feet below are slightly bluish-green, elliptical 4.7 x 2.4 cm., spinulose-dentate with 4-6 teeth per side; drying in mid-October and deciduous before 1 November; pubescence 1-6 rayed,

mostly 4 rayed on both surfaces.

Leaves of clone (76), 25 x 20 x 7 feet, 10 feet below (75) are bluish-green, oval 6.7 x 3.5 cm., spinulose-dentate with 3-4 rounded teeth per side; becoming dry and gradually deciduous after late October; pubescence 1-8 rayed, mostly 4, 5 rayed on both surfaces.

Leaves of clone (72), 20 x 10 x 7 feet, continuous with the lower portion of (76) and difficult to separate, are green, elliptical to obovate, 5.5 x 3.0 cm., spinulose-dentate with 3-4 teeth per side; gradually deciduous after late October; pubescence 1-5 rayed on the surface; 1-8 rayed beneath, predominately 4 rayed on both surfaces.

Leaves of clone (73), a backcross 4 x 4 x 4 feet, 10 feet below the lower edge of (76), are green, obovate 5.3 x 3.2 cm., with 3-5 frequently pointed lobes per side; sinuses shallow acute; deciduous before 1 November; pubescence sparse 1-5 rayed above; sparse 1-6 rayed mostly 5, 6 rayed beneath. Acorn production has been slight for the entire colony; none were produced in 1957.

South 24 miles on the Pahvant Mountains 4.7 miles southeast of Holden, clone #25 (69), 85 x 65 x 10 feet is growing on a gentle west exposure on top of a flat ridge 0.5 mile north from the mouth of Pioneer Creek Canyon at 6200 feet, (approximately 100 yards east-northeast from a single White fir lower on the ridge). Leaves are bluish-green above, pubescence sparse 1-8 rayed; yellow-green beneath, hairs dense 1-8 rayed, with

many 6-8 rayed; elliptical 4.5 x 2.5 cm., spinulose-dentate with 3-4 teeth per side; gradually losing color after late November, dry persistent in April. Acorn production has been slight. Deer were plentiful and had been within the clone, but only a few branches were browsed.

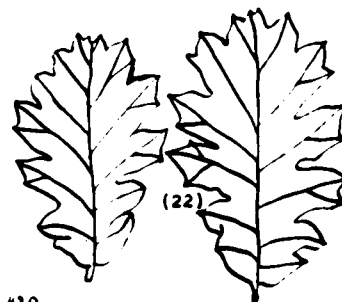
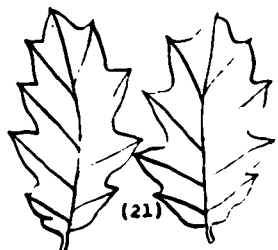
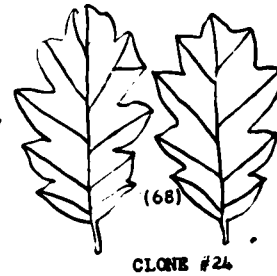
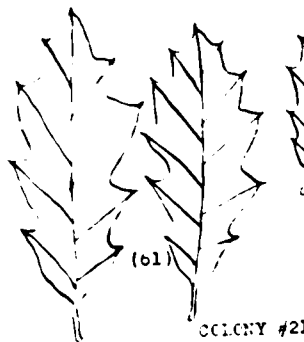
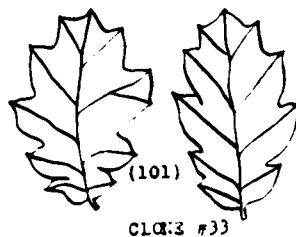
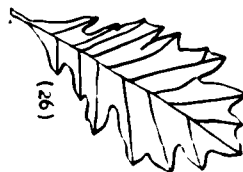
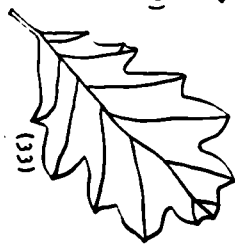
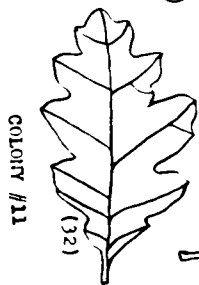
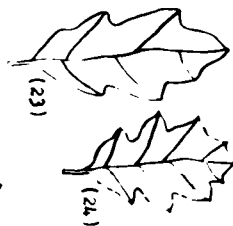
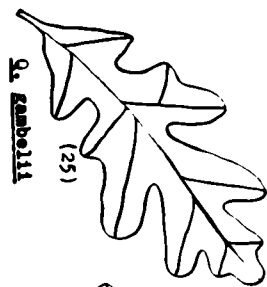
Southwest 32 miles, clone #26 (70), 25 x 8 x 10 feet is growing on a west exposure in Baker Canyon at 5700 feet, approximately 13.4 highway miles southwest of Kanosh, 60 feet east of the highway near a fence. Leaves are dark shiny green above, pubescence 1-8 rayed, mostly 4 rayed; light green beneath, hairs dense 1, 4-9 rayed; elliptical 5.2 x 2.5 cm., spinulose-dentate with 3-4 teeth per side; gradually drying in late November, some persistent in April. Past acorn production has been slight. Lower branches show heavy browsing by deer.

Southwest 27 miles to the Mineral Mountains, colony #30 (87) (88), 25 x 20 x 9 feet is growing on a southeast exposure near the base of a huge rock monolith, at 6200 feet. This site is located near the end of a continuous series of gigantic boulders projecting farthest west 4.0 miles north-northeast from clone #29, (4.6 miles north-northeast of the Beaver to Milford "Pass Road") 8.5 miles east of Milford. Leaves of the west portion, clone (87), a possible backcross, are green, oval to obovate 7.5 x 4.3 cm., thin textured with 4-5 deep frequently double pointed lobes per side; gradually deciduous after late November; pubescence 1-8 rayed, many 6-8 rayed on both surfaces.

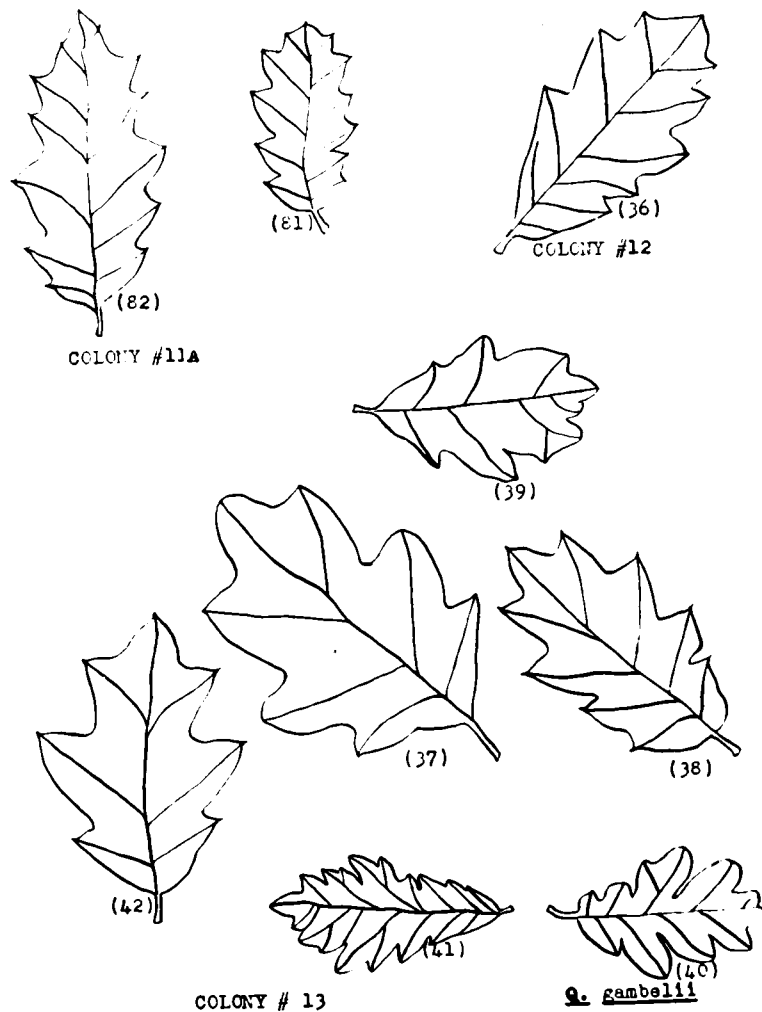
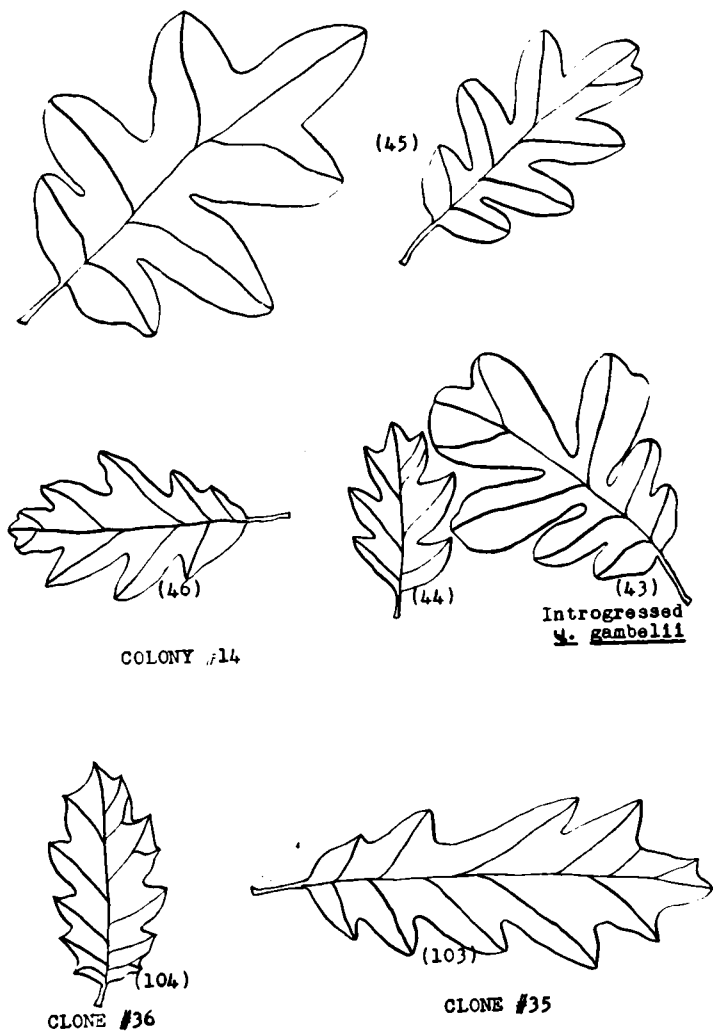
Leaves of the east portion, clone (88) are shiny green

above, pubescence 1-8 rayed; dull beneath, hairs 1-9 rayed; leathery elliptical 6.5 x 3.7 cm. with 3-4 deep, round or pointed lobes per side; gradually deciduous after late November. Past acorn production has been slight if any. Stem galls are present. Dead Juniper stumps nearby indicate an old fire, although some hybrid oak trunks are seven inches in diameter near the base.

Clone #29 (86), 25 x 20 x 10 feet, also burned by fire in the past marks the known southern limit of relic hybrids in the Great Basin. It is growing on a south exposure at 6100 feet protected by large boulders, 4 miles south of colony #30, (0.6 mile north of the Beaver to Milford "Pass Road") 7.5 miles east-southeast of Milford. Leaves are shiny green above, pubescence 3-8 rayed; dull beneath, hairs 1-10 rayed, mostly 8 rayed; elliptical 5.2 x 2.7 cm., spinulose-dentate with 3-4 teeth per side; gradually deciduous beginning in early November; bark is gray. Acorn production has been slight if any. Branches show heavy browsing by deer.

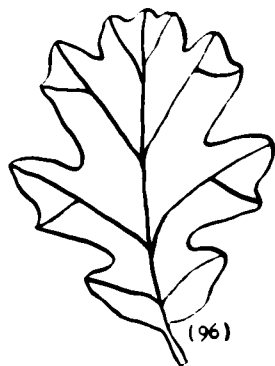


MORPHOLOGICAL DIFFERENCES OF LEAVES

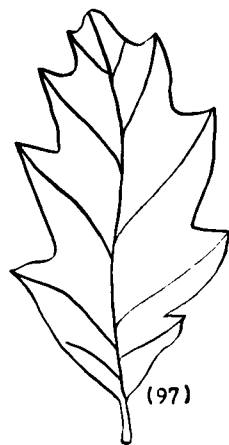




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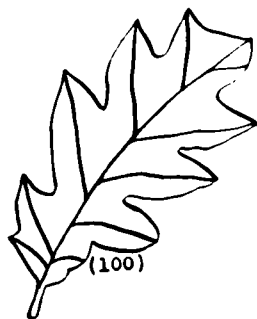
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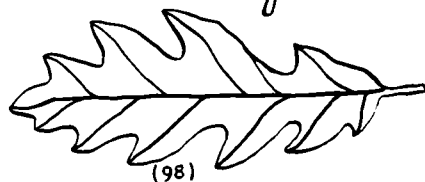
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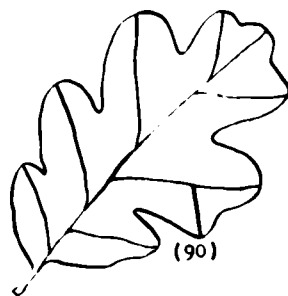


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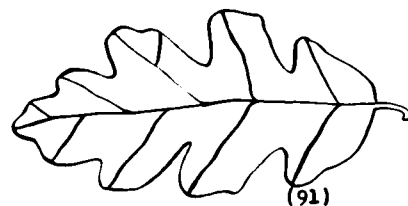


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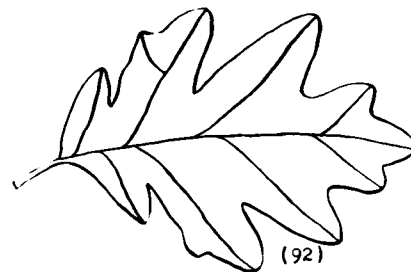
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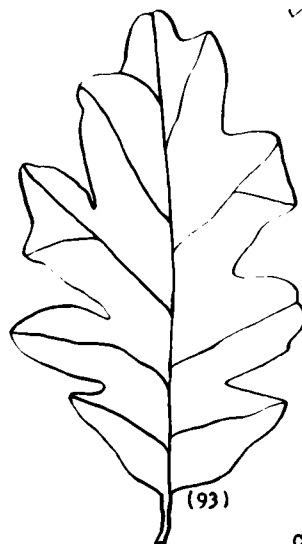
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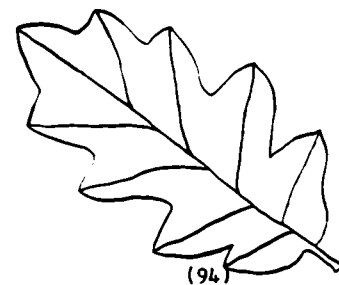
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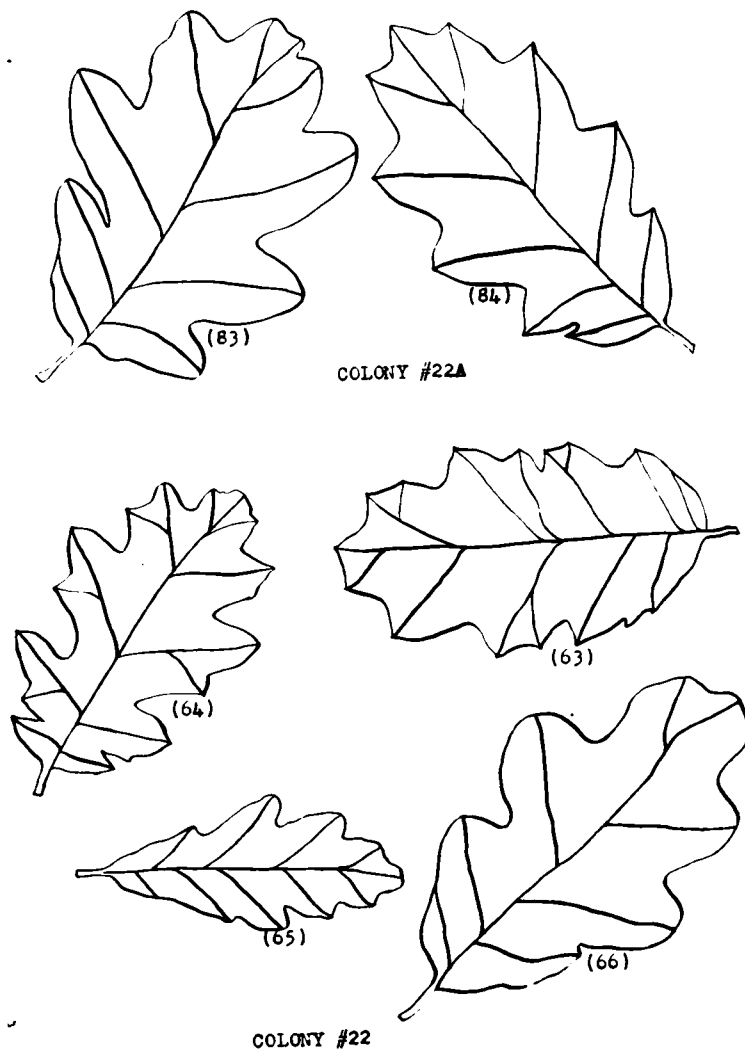
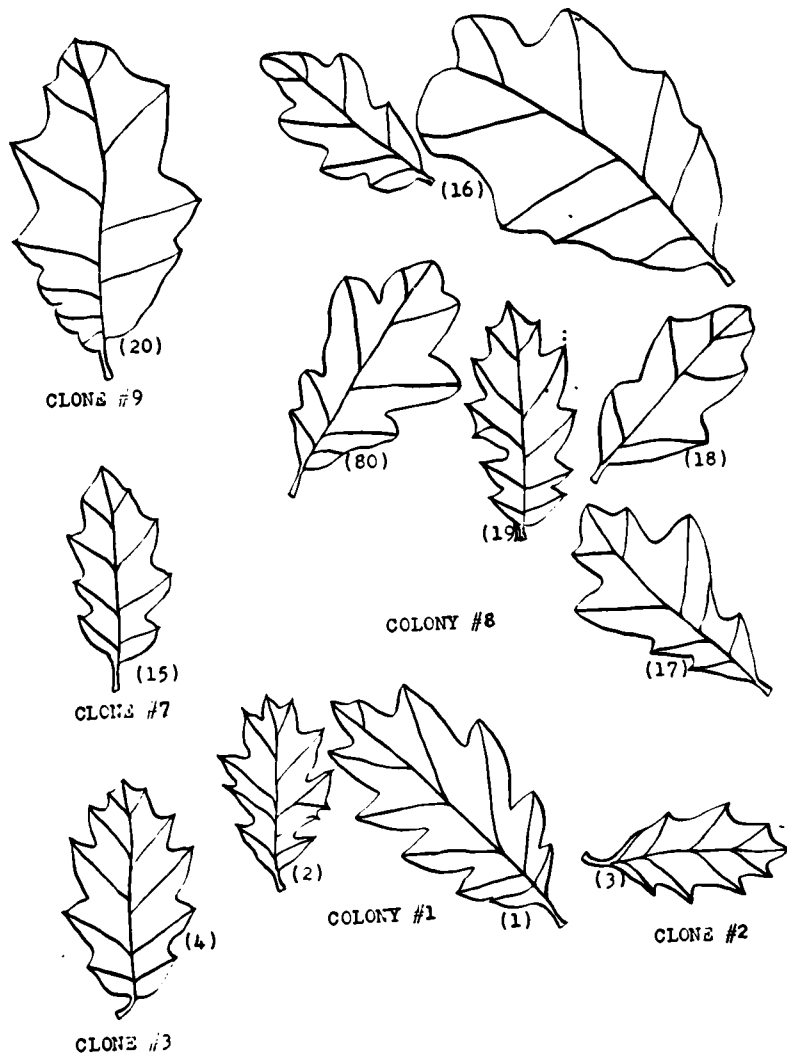


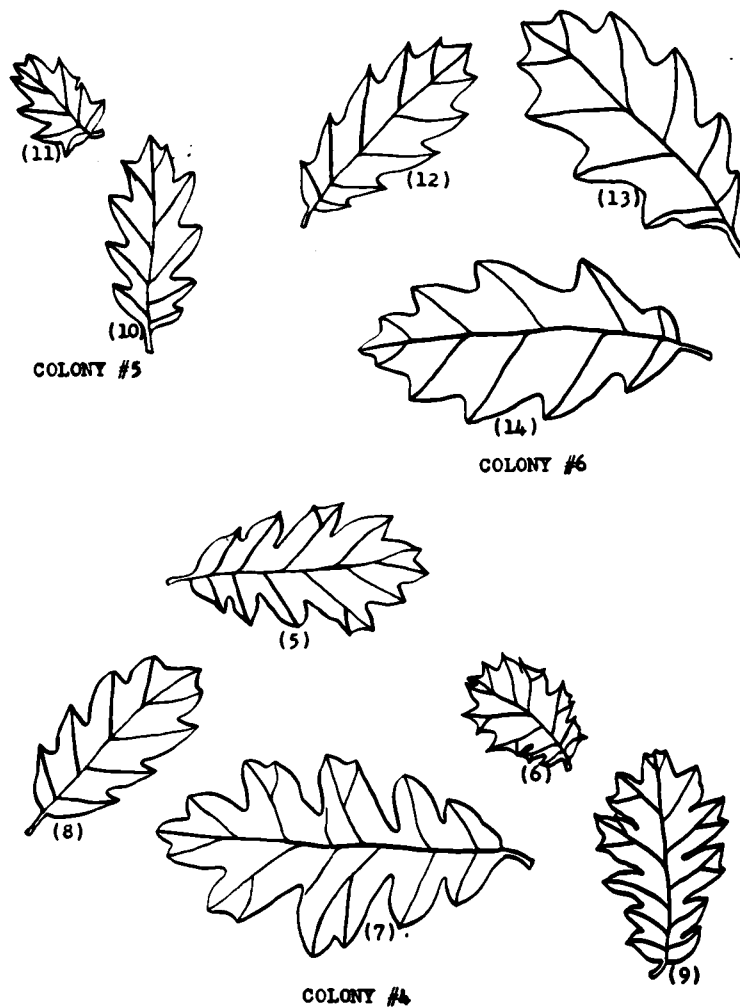
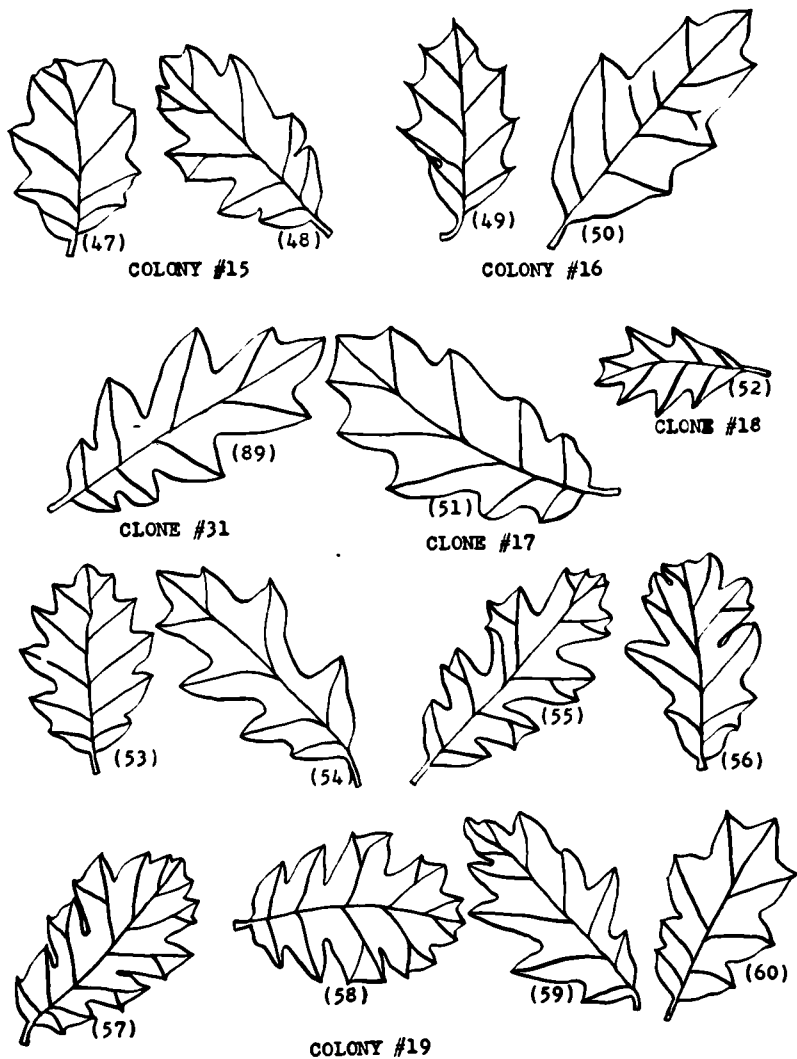
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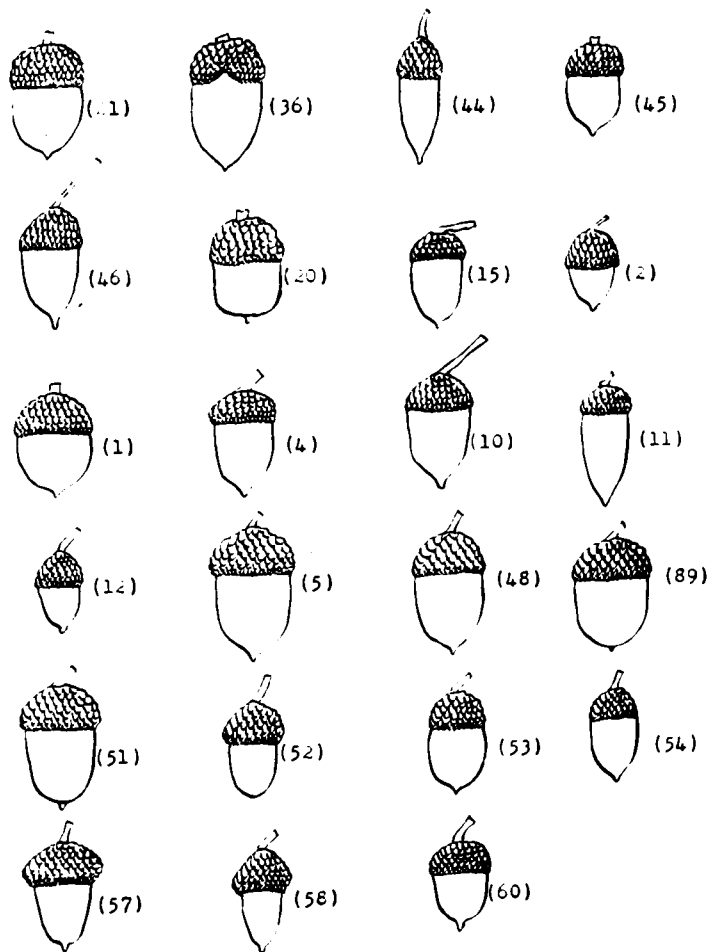


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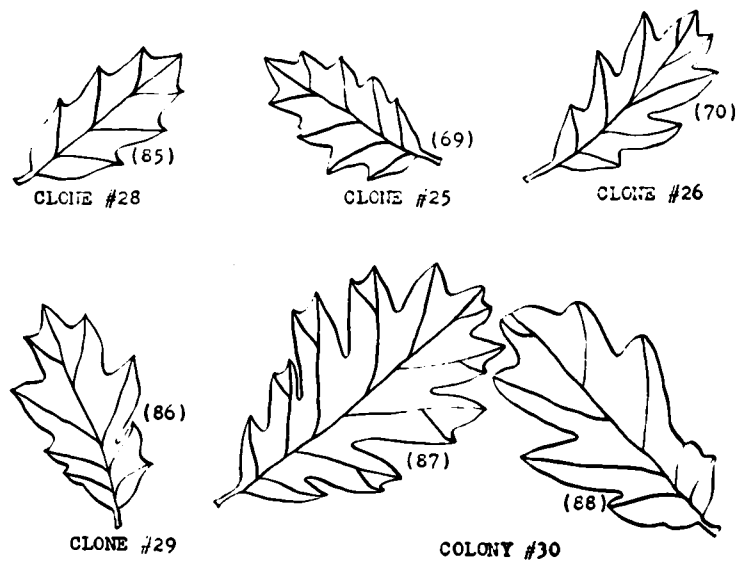
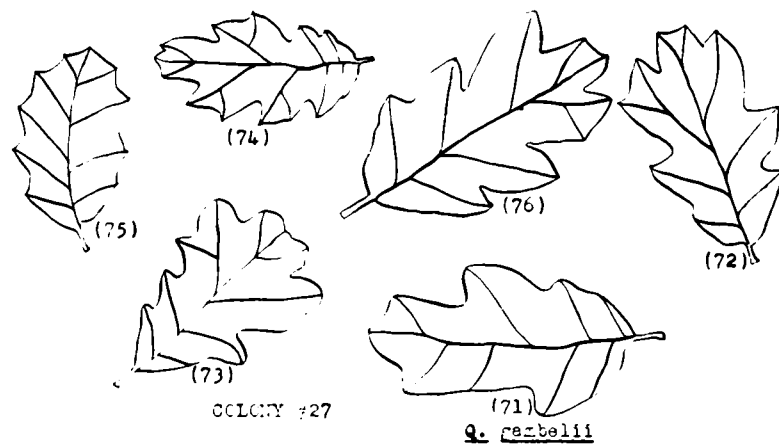
COLONY #32







MORPHOLOGICAL DIFFERENCES OF ACORNS



DISCUSSION OF ECOLOGICAL FEATURES

A. Environmental Factors

Distribution

The distribution of the Great Basin hybrid oaks is always discontinuous and the distance separating clones is highly variable, from less than one to as much as 30 to 50 miles. They are confined to the usual south to west exposures of foothills, within a generally narrow elevation range, which indicates that these hybrids are existing near their minimal temperature tolerance limits. The clones occur within an inversion belt where recurring warmer temperatures from inversion layers at night compensate for the general temperature decrease due to the periodic absence of sunshine. Colder air which settles in the valleys at night prevents the existence of any hybrid clones below their present lower limit 4600 feet, and the general temperature decrease above their upper limit 6900 feet, prevents these hybrids from growing at higher elevations. At the higher elevations of their range these clones are frequently protected by coves in or near limestone cliffs of obvious high thermal values. At lower elevations they occur in a generally open habitat.

Elevation Range

The average elevation of seventeen* hybrids on the Wasatch Mountains is 5475 feet; range is 4600 to 6700 feet. Twelve of

*18 minus one removed

these exist, within a narrow 600 foot zone, 300 feet above and below the mean figure line. The hybrid clone that existed at 4600 feet marked the lower limit of hybrids in the Great Basin.

On the Oquirrh Mountains the average of fifteen hybrids is 5760 feet; range is 5060 to 6900 feet. Eleven of the total are found within the 600 foot zone, while the average of eight hybrids on the west drainage, 5757 feet, is not significantly lower than the average for seven hybrids on the east drainage, 5765 feet, although the total average is 285 feet higher on the Oquirrh than on the Wasatch Mountains. The only two known hybrids on the Traverse Mountains are found at an elevation of 5400 feet.

The combined average elevation of six hybrids ranging from 5700 to 6400 feet, on the Sheeprock, Canyon, Pahvant, and Mineral Mountains is 6100 feet; 340 feet higher than the average on the Oquirrh Mountains, and 625 feet higher than the average on the Wasatch Mountains, although the two highest clones are found on the Oquirrh (6900 feet), and Wasatch Mountains (6700 feet) respectively.

This higher average elevation is closely associated with temperature inversions which are evidently influenced by relatively higher valley floors. Rush Valley near the hybrid site on the Sheeprock Mountains is approximately 5500 feet; the Sevier Desert near the Canyon Mountains, about 4500 feet; Black Rock Desert near the Pahvant Mountains about 4600 feet; and the

low point of the valley floor west of the Mineral Mountains is approximately 5000 feet. These hybrids indicate that during inversion, warmer layers of air rise to higher altitudes above relatively higher valley floors.

Temperature Inversions

The inversion phenomenon exerts the greatest environmental influence, and has permitted these restricted relic hybrid clones to persist in the Great Basin. Exposure without the temperature increase from the inversions, especially during the critical winter months with extended cold nights, would have undoubtedly terminated their existence long ago. The work of Dickson,¹⁰ illustrates this principle clearly. During the period August 1956 through May 1957 data compiled at five stations; Salt Lake Municipal Airport, 4220 feet; Salt Lake City 4260 feet; University of Utah, 4737 feet; Fort Douglas, 4940 feet; and the mouth of Red Butte Canyon, 5160 feet, revealed a total of 548 inversions. The valley inversions were distributed throughout the year, but reached a maximum during the winter months. Three hundred and forty-four of various depths occurred during a critical five month period; in October 67, November 78, December 79, January 61, and February 59. Of the total number of inversions, 212 occurred at 0230 A.M.; 162 at 0830 A.M.; 9 at 1430 P.M.; and 165 at 2030 P.M. The magnitude of inversion most frequent during the 10 months, was 3° Fahrenheit 102 times, 2° F. 90 times, and 4° F. 82 times. Shaw¹⁰

stated that with light winds and a clear sky, the inversions extend up to 1000 feet with a magnitude exceeding 9° Farenheit.

Higher maximum temperatures¹⁰ were registered consistently at the airport at 4220 feet, than at stations located at the University of Utah 4737 feet, Red Butte Canyon 5160 feet, and higher slopes. The airport is 3° to 4° Farenheit warmer in winter, and 5 to 7 degrees warmer in summer.

The mean value for lapse nights¹⁰ (without inversion) was nearly the same as the usual rate of temperature decrease, 1° Farenheit per 300 feet increase in elevation. The mean of the valley inversion nights shows that the valley was an average 3.5° Farenheit colder than the University of Utah, and 5 degrees colder than Red Butte Canyon on such nights. In Salt Lake City, during the last week in February and the first week in March, 1957, the University of Utah recorded a minimum of 39° Farenheit and a minimum of 27° Farenheit was recorded at the airport, a difference of 12 degrees.

Temperature Requirements

Nearly all relic clones receive a majority of direct sunshine with west, south or southwest exposures reradiating considerable warmth after exposure to the sun during its greatest intensity. Direct sunshine during the day and temperature increase from inversions of warmer air at night are the basic factors supporting the existence of all relic hybrids.

Data compiled by Cottam⁹ during the period 21 March 1956 through 19 March 1957 shows significant differences in annual

average maximum, minimum and mean temperatures for the following oak-species combinations. The figures of approximate elevation range indicate the extent of the vegetation belt in which the greatest density of the various oak-species combinations occurs. Locations of the thermal stations are shown in plate 2.

Oak Species	Elev. Range (approx.)	Ave. Max. Temp. °F.	Ave. Min. Temp. °F.	Ave. Mean Temp. °F.
Relic Hybrids and <u>Q. gambelii</u>	500	65.1	42.1	53.6
Hybrids and both parents	1000	68.7	36.6	52.6
<u>Q. turbinella</u>	2000	75.5	46.5	61.0
<u>Q. gambelii</u>	2000	59.6	32.8	46.2

TABLE 1

These figures show that the average mean temperature for relic hybrids is intermediate between those for Q. turbinella and Q. gambelii. The annual average mean temperature for relic hybrids is 1° Fahrenheit warmer, and the years average minimum temperature is 5.5° F. warmer than for hybrids and both parents in extreme southwestern Utah and northern Arizona. However, during the critical winter months the average minimum temperatures⁹ for hybrids and both parents are warmer than the average for the relic hybrids. Therefore, colder average minimum temperatures at the relic hybrid sites in winter account for the

absence of Q. turbinella.

Soils

All clones are growing on rocky slopes in well drained soils ranging from rocky clay and sandy loams, to gravel loams, all with only average amounts of organic matter. On the Oquirrh Mountains nearly all clones are closely associated with limestone outcrops, while on the Wasatch Mountains many clones are growing in porous soils derived from quartzites as well as in limestone rocks. The drainage properties and organic content are important although probably not limiting factors.

Water Relationships

Sufficient data is not available to determine the minimum moisture requirements of these hybrids. It is probable that these requirements are intermediate between those of the parents. Christensen⁸ lists 15 inches annual precipitation as the minimum requirements of Q. gambelii. The hybrids would thus require slightly less because they are growing on dry hillsides at the lower limits of Gambel oak, and Q. turbinella, an amount relatively less than the hybrids, because its optimum growth is attained at elevations generally lower than the hybrids. At the northern latitudes in the Great Basin, there is no evidence that the amount of precipitation is a factor limiting the distribution of the relic hybrids.

B. Growth and Age

Assuming that the growth rate is no greater, or not much greater than Gambel oak, 4 inches per year,⁸ several hundred years would be necessary to account for the size of these vegetatively reproduced relic clones, as large as 250 x 150 feet. Because many clones have been completely burned by fire, they are older than their present regrowth indicates. The present height of clone (2), ten feet, represents regrowth since the fire of 1920. The size of these larger clones precludes the possibility of any new introduction into the area. The absence of the live oak parent from the relic hybrid sites since the introduction of the present climate, based on average minimum temperatures⁹, extends the origin of these relic hybrid clones back thousands of years to an earlier climatic period warmer than the present when conditions were suitable for migration and growth of Q. turbinella.

C. Climatological Changes

A basic question ultimately arises. During what climatic period did the heat requiring live oak Quercus turbinella make its northward migration nearly to the present northern limits of Quercus gambelii?

According to Antevs³, the glacial period ended about 10,000 years ago, when the temperature was slightly cooler than the present. Following, there was an Anathermal period of increasing

warmth for 2,500 years; an Altithermal period of 3,500 years, during which time glaciers completely disappeared in the western mountains, because the highest mean temperature reached was nearly 4° F. warmer than present; and a relatively cool Medithermal period of 4000 years reaching to the present.³

A relatively cool and moist age began about 2000 B.C. In 1850 A.D. glaciers in the high western mountains attained their greatest extent of the past 10,000 years.² The Great Basin lakes in Utah and Nevada were low, but rose rapidly from 1860 to 1870. Great Salt Lake in 1867 submerged an old stormline at 4207 feet, which in 1850 formed the lower limit of sagebrush growth. Since saline soil will not support sagebrush, Gilbert² concluded that the lake had not been above this stormline for several hundred years prior to 1850. The maximum lake level of 4211.5 feet occurred in 1873.

The relationship between the maxima of glaciers in the high mountains and lakes in the adjacent basins was apparently an interaction of temperature, snow, and rain. Before 1850 the seasons in the high mountains may have been cool and short, producing a large amount of snow with restricted melting. Longer and warmer seasons after 1850 probably caused a great percentage of rain at high altitudes and a considerable and rapid melting of snow and glacier ice, resulting in abnormally large runoff which caused the exceptional rise of the lakes, for

"judging from the tree growth at the lower dry limit of the forest, the precipitation at this level 5000 to 6000 feet above the seas was from 1850 to 1916 only in some regions (Oregon) above the average of the past few hundred years".²

From more recent work, Antevs³ concluded that the climate during any part of the Post Pluvial which covers a period of the last 9000 years, has been only slightly more moist than at present.

The presence of these relic hybrid clones within the Great Basin always associated with Gambel oak, supports the theory that Quercus turbinella migrated north from the vicinity of the Pine Valley Mountains during the Altithermal period contemporaneously with the general northward migration of Quercus gambelii. The live oak possibly inhabited lower elevations along the foothills and hybridized freely with Gambel oak at or near the sites where the relic hybrids are found today. Only during a period of general temperature increase could the live oak have reached this extreme northern limit 300 miles north of its present range. The onset of colder winter temperatures accompanying the Medithermal period probably eliminated the live oak from the Great Basin, except for a few clones in the extreme southern portion.

The midrib gall wasps Andricus reticulatus, which presumably followed the live oak Q. turbinella, nearly to its limit in northern Utah during the Altithermal period exist only in three isolated populations of hybrids today, and are the only other living indicators of the once continuous flora and fauna that existed here during the Altithermal period. The greatest majority of them probably perished with their live oak hosts during the Medithermal period.

That various other biota occupied more northern and western areas in Utah than are inhabited today is evidenced by additional floral and faunal remains in Oak Creek Canyon less than one mile from #27 colony of hybrid oak in the Canyon Mountains. The spring runoff of flood proportion in 1952 exposed various strata beneath Oak Creek in the canyon bottom. W. Leslie Robinette discovered numerous stumps along the present stream course 20 feet below the original level, in the vicinity of the ranger station at 6000 feet elevation. Specimens of a few stumps were tentatively identified as Fremont cottonwood, Populus Fremontii Wats., which apparently is completely lacking on this mountain range today. Lower in the side of the wash, between the lower limit of Narrow-leaf cottonwoods and the forest boundary sign, at 5600 feet, Mr. Robinette discovered bones of the wild turkey, Meleagris sp., four feet below the surface developed soil layer in alluvium. This discovery is believed to be a new record for the Great Basin and Utah since the present range of the wild turkey in the west is found in the mountains of southeastern Arizona, New Mexico, southern Colorado, and western Texas, at the nearest point, 250 miles from this site.

Observation by the author revealed more bones protruding from the side of the wash in alluvial deposits 3 to 9 feet below the surface. The specimens include a rib and humerus from bison, Bison bison, a molar tooth in a portion of jaw and the upper part of a Bighorn sheep skull, Ovis canadensis. It is interesting to note that bison and Bighorn sheep are completely

absent from this range. A similar skull was found partially exposed on a high peak of the Oquirrh Mountains, and some mandibles of the Bighorn sheep and skeletal remains of other animals and birds were excavated from Marmot Cave, located near the mouth of Parley's Canyon at approximately 6000 feet in the Wasatch Mountains, where Bighorn sheep are also lacking today. These remnants indicate to a degree, some additional floral and faunal changes that have transpired in this area.

D. Gall Wasps

Parasitism

For three consecutive years, 1954-55-56, four host clones were parasitized by the midrib gall wasp Andricus reticulatus, but were free of any new midrib galls in 1957. Most species of gall wasps have histories which involve an alternation of generations, and cycles of a year or more. All Cynipidae inhabiting oaks have a regular alternation of bisexual and "agamic" (parthenogenetic) generations.¹⁸

Galls were collected December 5, 1954 and stored at normal room temperature (75° Fahrenheit). Eleven days later the tiny gall-formers²⁵, less than 3 mm. long, all females, red with black eyes, began to emerge. Also within these galls from the representative clones, were chalcid flies, smaller and black with red eyes, present in greater numbers than the gall wasps which they presumably parasitize. Brewster⁶ states that many wasps of the family Chalcididae parasitize true gall makers in the

egg and larval stages. The gall A. reticulatus is nearly round 7-10 mm. dark brown, hard, woody, with many cells not separable from the woody fiber radiating from a common center. It forms near the leaf base and protects both species of wasps. Upon hatching, the Chalcid larvae may feed on the Cynipid eggs or larvae, or both, and may eventually complete development in the gall in place of the host species. Under normal conditions the gall formers emerge in April or May and presumably reinfest the young plastic tissues (leaves) which are greatly preferred by gall producers.¹² The galls usually begin development in early May.

Brewster⁶ cites Kinsey who observed thousands of adults of numerous species and learned that the average length of life of the adult is approximately two days; while in many species, the adults die within a few minutes after oviposition, even though oviposition takes place within a few hours after emergence from the gall. Because the adults are physically weak, sudden changes in temperature or rainy periods may be fatal, or prevent the female from ovipositing. The absence of any new galls in 1957 is undoubtedly due to the alternating generation, which may produce galls on the roots,²¹ although the abnormally cool wet spring may have exerted considerable adverse effects. There are probably more than 600 oak galls occurring upon American oaks and as yet the direct connection between the alternating generations has been established for a relatively few.¹²

The presence today of these gall wasps nearly to the northern

extent of the ancient Quercus turbinella migration substantiates the fact that a continuous, mixed oak flora similar to that of central and southern Arizona and/or New Mexico existed in northern Utah during the Altithermal period to afford "stepping stones" for these wasps with such limited flight ability.

Distribution

The field notes of Weld²⁷ list the following hosts and locations where these insects are more common today. At Alpine, Texas, south of Carlsbad, New Mexico, these galls were observed on Q. grisea Liebm. In New Mexico they were collected: on Q. gambelii Nutt. at Fierro, Las Vegas Hot Springs, Tijeras, Magdalena, and Glorieta; on Q. fendleri Liebm. at Magdalena, Glorieta, Las Vegas Hot Springs and Bandalier National Monument; on Q. pungens Liebm. at Hillsboro, Socorro, Tijeras and Bard; on Q. grisea Liebm. at Magdalena, Tijeras, Fierro and Wagon Mound; on Q. undulata Torr. at Socorro; and on Q. reticulata = diversicolor Trel. at Kingston. In Arizona they were collected on Q. grisea Liebm. at Williams, Prescott, and Wolf Creek Camp; on Q. arizonica Sarg. at Oracle, Bisbee; Patagonia, and Wolf Creek Camp; on Q. oblongifolia Torr. at Nogales; on Q. toumeyi Sarg. at Patagonia; on Q. subturbinella = turbinella Greene. at Pine; and on Q. pungens Liebm. at Ashfork, Hackberry; and Campcreek. In all states, locations are south of 36° north latitude.

In Utah this species of wasp has been collected previously, only at Zion Canyon, and the host was Q. turbinella. Recent

records from these relic hybrids, Q. gambelii x Q. turbinella, establish sites at Alpine on the Wasatch Mountains and Harker's Canyon on the Oquirrh Mountains, 225 miles north of Zion Canyon and 350 miles north of Hackberry and Williams, Arizona. They have been reported from Q. gambelii in New Mexico, but have never been reported from this host in Arizona or Utah.²⁷ This sparse distribution suggests that the record at Zion Canyon may also be an isolated relic population.

Isolation

According to Kinsey¹⁷ there are two isolating mechanisms which account for diverse populations of Cynipidae, geographic distance, the main mechanism, and host isolation. More than 90 per cent of all Cynipidae occur on oaks. Each local population is restricted to a single species of oak host, or at most to a small group of very closely related oaks. Kinsey states,

"In gathering more than five million galls made by the Cynipidae, we have never found an instance of a single individual living on anything but its normal host. In these insects, this host isolation is effected by way of the animal's chemical sense, which is delicate enough to allow it to make distinctions between closely related hosts and critical enough to prevent it from ovipositing on any but the single species of oak."

Earlier work by Kinsey¹⁶ stated that unless the hosts occur in a fairly continuous or pure stand, which is not usual for most species of oak, the insects are handicapped in their spread. Whether fully winged or subapterous, the insects move about almost entirely by using their legs. Sensory chemotrophic

reactions which lead them to oviposit at particular spots on specific hosts, usually keep them from wandering off the tree on which they were raised. Even when the branches of several trees of one species of oak intertwine, one tree may be loaded with galls while others in the stand are nearly or entirely free of galls.

Hubbs and Miller¹³ assume that certain oaks and their associated gall wasps, characteristic of the California region, must have crossed the now oakless intervening deserts to reach their present locations on the mountains to the east, during the last Pluvial period when conditions were suitable for wide dispersal of floras and faunas. However, data compiled within this account indicates that these midrib gall wasps migrated in a south to north direction along mountain ranges where hosts were available after the Pluvial, rather than crossing deserts from west to east during the wet period.

Stem Galls

Stem galls Disholcaspis rubens Gill., round smooth or rough galls one-half inch in diameter and usually light straw color tinted with red,¹² are present on small twigs of a few F₁ hybrid clones, and are more numerous on backcrosses to Gambel oak. Their preference could also be a result of the physiochemical makeup of the host since they are common on Q. gambelii Nutt., and have been reported on Q. undulata Torr. at Manitou, Colorado. These wasps emerge from the gall in late fall. During the larval stage they are also parasitized by Chalcid wasps.²⁷

Surface Leaf Galls

Another gall, Xanthoteras eberneum Bass.,²⁷ a small one-quarter inch, orange globular growth on either or both leaf surfaces is also present on a few F₁ hybrids, but more numerous on backcrosses with evident characters similar to Gambel oak. It is one of the commonest galls on all the White Oaks of the Great Basin. The agamic generation was collected in early November from clone #28 on the Sheeprock Mountains. The wasps emerge in late fall, but where they oviposit is not known. There is probably an alternating bisexual generation in early spring, on or in buds, on flowers or very young leaves. Their life cycle has never been worked out.²⁷

E. Environmental Restrictions, Parasitism of Acorns

A prime example of the destructive effects of insects is illustrated with clone #5 (10), which produced approximately 7000 acorns in 1957. Approximately ninety-eight per cent were parasitized by larvae of the Nut and Acorn weevil and the Catalina cherry moth. This same degree of parasitism existed within all other hybrid clones as well as the surrounding Gambel oak, and is presently the greatest single factor preventing acorn germination. Harvest in autumn by squirrels and chipmunks further prevents the slight marginal chances of the few unparasitized nuts ever reaching a suitable germination site. Of the total 40 colonies, only 5 seedlings, which grew under natural habitat conditions have been observed thus far.

Catalina Cherry Moth

Larvae of the Catalina Cherry moth Melissopus latiferreanus Wlsm., Family, Olethreutidae; also known as Filbertworms in the larval stage,²⁰ are 10-25 mm. in length and nearly white, the three distinct thoracic segments each bearing true segmented legs. The head with chewing mouth parts, opposable mandibles, is reddish brown. They infest various nuts, especially filberts, wild hazel nuts, and acorns; and such fruits as apple, pear, peach, cherry and strawberry.

Essig¹¹ reports infestations of the Catalina cherry in southern California and the large green galls of Andricus californicus Bass. on Blue oak in central California. The eggs are laid on the surface of the fruit and galls and after development the larvae hibernate in a cocoon in the soil under the Catalina cherry, but it has not been determined if they leave the oak galls or hibernate within. There is but one brood. The adult has an expanse of 12-15 mm., and is pale or dusky-bronze, with two coppery areas at the tips of the forewings. They range from Maine to California.

Nut and Acorn Weevil

Larvae of the Nut and Acorn weevil, Curculio strictus Casey, are seriously destructive to acorns, chestnuts, hickory and filbert nuts, in addition to plum, tomato, apple, strawberry, cotton, clover, alfalfa and pine. They belong to the Family Curculionidae, Sub-Order Rhynchophora, and are distinguished by the extremely long and slender rostrum or beak, and

vertical mandibles.⁷ The beak is used by the female for drilling holes in nuts or acorns through which the eggs are deposited. Eggs are laid in the nuts from June to September. The developing larvae, white maggot-like grubs always without legs, consume the endosperm with their strong heavy jaws. After the nuts fall to the ground in September, the full grown larvae 14 mm. in length, leave the shell and burrow into the ground and fashion a small cell in which they pass the winter. In early summer the adults, gray, about one-half inch in length, emerge, and lay eggs in the young nuts to repeat the cycle.⁴ This weevil is known generally from oaks in eastern United States, but has been collected at Colorado Springs, Manitou and Ouray in Colorado; Las Vegas, New Mexico; Williams, Arizona; and Millcreek, American Fork, Provo and Stockton, Utah.⁷

Interesting observations have been made on the natural enemies of the nut weevils. The Shorttail shrew finds and eats the larvae in the ground beneath nut bearing trees. Squirrels gathering acorns, eat the larvae within as well as storing the nuts for winter use.⁴

F. Germination Study, Viability of Acorns

In early September acorns were gathered from all producing relic hybrid clones and also from Q. turbinella, Q. gambelii and hybrids on the Pine Valley Mountains. They were stored at 3° Centigrade for 4 weeks. The greatest concern was to kill the moth and weevil larvae, but the cold temperature did not accomplish this. Cold stratification of the nuts depletes or

destroys a chemical inhibitor of growth in the endosperm, making possible germination and growth of the embryo. The reaction is a curious one because it proceeds more rapidly at low than at high temperatures.⁵

Johnson¹⁴ reports that acorn size influences the percentage of germination. Large acorns often contain two embryos. Six viable embryos may be found in one acorn.

Weight per 1000 acorns (Kg)	9.20	5.34	3.94	3.12	2.12
No. plants per 100 acorns	125	79	94	89	73

Approximately one half the representative acorns were sent to Dr. Tucker at the University of California, Davis, and the remainder planted in the greenhouse at the University of Utah. Good germination results were obtained from the entire collection. Acorns from numerous relic clones germinated after four weeks cold storage and many seedlings are presently growing from: clone #3 (4), #5 (10), #10 (21), #15 (48) F₃ generation, #17 (51), #19 (53) and #20 (60). A higher percentage of acorns germinated after 13 weeks cold storage and numerous young seedlings are growing from: clone #1 (1) F₃ generation, #3 (4), #4 (5), #5 (10) and (11), #10 (21), #15 (48) F₃ generation, #17 (51), #18 (52), #19 (53) and (54) F₃ generation, and #20 (60). The variable hybrid characteristics exhibited by these seedlings result from self-pollination, cross-pollination and/or pollination by Gambel oak.

Acorns from Gambel oak immediately surrounding various relic hybrid clones did not germinate. Good results were obtained from

those growing on the Pine Valley Mountains, and some seedlings exhibit what appear to be hybrid characteristics resulting from evident pollination by Q. turbinella and/or F_1 hybrids.

Acorns from Q. turbinella produced seedlings nearly identical to the parent plant, indicating self or cross-pollination from other clones of Q. turbinella. It is not known if Q. gambelii can successfully pollinate Q. turbinella to form viable acorns, although present evidence indicates that F_1 hybrids may be formed by Q. turbinella pollinating Q. gambelii. It may be significant to learn which species or plants contribute the pollen to form these various hybrids and backcrosses.

It is difficult to discern hybrid characteristics from pure-pollinated strains in young seedlings, especially those grown under controlled conditions. The smaller stiff, sharp-spined leaves of the live oak parent are more readily distinguishable, but young leaves of relic hybrids and backcrosses are frequently so similar to Gambel oak, that their identification presents a challenge to the most critical observer.

If subsequent germination studies are undertaken, acorns must be gathered prior to 1 September to prevent them from being harvested by squirrels and chipmunks; fumigated with Bisulphide of Carbon⁴, or other fumigant to kill the insect larvae within and placed in refrigeration. Four weeks is not adequate, although a few from clone #5 (10) germinated in cold storage after 21 days. Others planted after 13 weeks refrigeration, exhibited a higher percentage of germination and more

vigorous growth. Optimum results can be obtained if shells are removed prior to planting, for in some examples the shell prevents the embryo from breaking through the apex, in which case the endosperm may be forced out through the base, delaying or preventing growth. Stratification at various temperatures and durations would undoubtedly reveal the degree and exposure for optimum germination and growth.

SUMMARY

1. Forty relic colonies of the hybrid oak Quercus gambelii Nutt. x Quercus turbinella Greene have been located. They are distributed on seven mountain ranges bordering the eastern limits of prehistoric Lake Bonneville and along the western continuous limits of Gambel oak in northern and central Utah, at elevations from 4600 to 6900 feet. Probably more colonies exist in the Great Basin.
2. The morphologically similar individuals comprising a thicket, and the fact that the individuals all appear to sprout from a common root mass, indicate that each thicket is actually one clone. The growth rate of such clones indicates that they are hundreds and possibly several thousand years old.
3. The different clones exhibit morphological and physiological differences which suggests that they represent not only intermediate F_1 type hybrids, but also later generation backcrosses. They exhibit moderate fertility, but parasitism of acorns by insect larvae limits the establishment of new hybrid derivatives.
4. Temperature studies indicate that Q. turbinella requires average mean temperatures that are 15° Farenheit warmer than those required by Q. gambelii. The hybrids require intermediate average mean temperatures. The hybrid clones occur usually on south to west-facing slopes at elevations that are appreciably warmer than usual due to frequent temperature

inversions. No habitats with temperatures suitably warm for Q. turbinella have been found north of Kanarraville, the present distributional limit of that species.

5. The evidence presented suggests to the author that the hybrid clones here described are relics of a previous warmer era, the Altithermal period, when the live oak parent Q. turbinella, was present in the region where the hybrids still persist. The subsequent decrease in temperature of the Medithermal period killed the Q. turbinella parent. Only hybrid clones with suitable physiological characteristics that happened to be growing in locally warmer niches were able to persist. They have persisted vegetatively or with occasional backcrossing to Q. gambelii apparently from the Altithermal period to the present time.
6. Evidence from the host specific parasitic wasps of this group supports these conclusions.

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